2009

Spatial and Temporal variability of macroinvertyebrate communities in vernal pools on the Coastal Plain of Virginia

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University,

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July, 2009

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Acknowledgement

I would like to express deep sense of gratitude to all who contributed to the successful completion of this Master's thesis.

I would like to acknowledge my advisor Dr. Leonard Smock, Professor and Chairman of the Department of Biology, College of Humanities & Sciences, Virginia Commonwealth University, Richmond, VA, USA, who encouraged and enabled me through my research to accomplish this goal. I owe my content to the innumerable interactions I have had with my advisor unearthing concepts I included in my work.

I extend my thanks to my committee members, Dr. Donald Young, Dr. Paul Bukaveckas, Dr. D'Arcy Mays, for their time and advice.

This work would not be complete without the unrelenting support of my laboratory peers, Andrew Garey and Holly Houtz. I appreciate Ralphaell Do, Anu Kuriakose and Arco Paul for sacrificing their personal time assisting me in field work. This also goes out to Anne Wright who helped me with new ideas.

I would like to dedicate this work to my mother, Sumitra Ganguly, for leading her children into intellectual pursuits and to my father, Sukdev Ganguly, for those uncompromising principles that have guided me through my life. I cannot forget my older sister, Shilpi Ganguly, who has always been my unwavering wall of support.

I wish to end by recalling my faith in GOD throughout this stimulating exercise without which I would not have arrived at this closure.

Thank you.

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Abstract

Vernal pools are often defined as seasonal pools that typically are inundated beginning in the winter and then drying out completely in summer. Though evidence of spatial and temporal variability in the macroinvertebrate communities of vernal pools has been found in previous studies, it has not been studied extensively. The primary objective of this study was to determine the extent of variability in the macroinvertebrate communities within vernal pools closely situated in a forested landscape. An effort was made to explain this variability with respect to certain physiochemical environmental variables of the pools.

Significant variability was observed in the macroinvertebrate communities within the vernal pools both spatially and temporally. Water temperature, as an indicator of seasonal changes, was strongly correlated with the observed variations. Higher species richness and diversity were observed in the pools in winter than in spring 2007. Chironomidae was the most diverse family (8 genera) occurring in these vernal pools. At the beginning of inundation, amphipods and copepods were more abundant. β-diversity was low in both winter and spring 2007; α-diversity in winter was high and low in spring 2007.

INTRODUCTION

The United States government, until recently, issued policies supporting the draining and filling of wetlands for agricultural or other such purposes. Recently, the ecological importance of wetlands has been recognized, including their services such as reducing effects of floodwaters, improving water quality and providing habitat for aquatic plants and animals (*Daily 1997; Sharitz & Batzer 1999*). According to the Supreme Court decision (*SWANCC*), 'isolated' wetlands are not included in the 'waters of United States'. Even though this decision places the 'isolated' wetlands under risk, vernal pools remain among the least studied and understood 'isolated' wetlands.

The term 'vernal pool' was first used in 1920 to name ephemerally wet depressions (*Zedler 1987*). Certain federal agencies classified most vernal pools as isolated depressional wetlands, riparian depressions or slope wetlands (*Colburn 2004*). The US Fish & Wildlife Service (USFWS) classified vernal pools as seasonal palustrine wetlands due to their shallow depths and periodic dry phase (*Cowardin et al. 1979*). Several ecologists tried to classify vernal pools primarily on their hydrologic conditions, describing these pools as 'short cycle pools' which typically fill up with rainwater, surface runoff or groundwater from late fall to early spring then drying up completely in late spring to early summer and with new plant growth and resultant increased evapo-transpiration (*Masters 1968; Wiggins et al. 1980; Colburn 2004*). To include other variations in the hydrology of these pools, Zedler (2003) classified vernal pools as a subset of ephemeral wetlands that are small, form reliably in a permanent basin and dry reliably to maintain a level of moisture as dry as the surrounding uplands (*Zedler 2003*).

This definition of vernal pools, however, did not apply to forested or disturbance oriented pools. A more encompassing classification is provided by the US Environmental Protection Agency (*Brown and Jung 2005*) based on the following five characteristics:-

- Vernal pools occur in or next to forests or other wooded areas (woodland context);
- Vernal pools lie in confined basins with no continuous inlet or outlet and do not have a continuous surface water connection with permanently flooded waters (isolation);
- Vernal pools are typically small and shallow;
- Vernal pools fill seasonally, with maximum water in spring and water level dropping substantially or totally in summer; the pools contain water for a minimum of two months in most years;
- Vernal pools lack established fish populations and hence provide critical habitat for those animals which are predation intolerant and for those organisms which are adapted to seasonal drawdown.

These characteristics often differ due to regional climatic patterns, characteristics of each pool's depression, and its watershed (Brooks *& Hayashi 2002, Winter & LaBaugh 2003, Brown & Jung 2005*). Therefore, ecologists tend to alter the definition to suit the vernal pools of the respective regions being studied. For instance, descriptions of vernal pools in Massachusetts and Wisconsin take the lush herbaceous growth of the dry phase into account (*Zedler 2003*), whereas vernal pools in Maine include forested wetlands whose vegetation does not differ from other wetlands (*Calhoun et al. 2003, Zedler 2003*). Keeley and Zedler (1998) mention that, pools in non – Mediterranean climates dry when climate reaches desert extremes (*Zedler 2003*). These characteristics (and their variations) of vernal pools can have a significant influence on the diversity of the aquatic macroinvertebrate communities of the pools.

As is seen by the descriptions of the ephemerally wet depressions or 'isolated' wetlands / vernal pools, the most dominant characteristic of a vernal pool is its hydrologic regime or hydroperiod. The hydroperiod of a vernal pool is greatly influenced by the seasonal input/output relationships of water of the region (*Brooks 2000, Zedler 2003*). The seasonal water input to these pools can range from fall precipitation to spring snowmelt/precipitation, followed by total desiccation in summer (*Wiggins et al. 1980, Brooks 2000*). For instance, all northeastern vernal pools are fed by late winter to early spring precipitation (*Schneider and Frost 1996, Colburn 2004*); whereas California pools are fed by strong winter rains (*Zedler 2003*). Both of these precipitation-fed systems may have other factors that could affect the hydroperiod such as low winter and spring temperatures and a shorter day length which in turn contributes to the reduced rate of evapotranspiration. Again, these may not be the only variables affecting the hydrologic regime of vernal pools.

Like all 'isolated' wetlands, the diversity seen in vernal pools depends greatly on factors (also known as 'island characteristics') such as proximity to a watershed and pool depth and size (*Hall et al. 2004*). The 'island biogeography' theory that faunal richness is directly proportional to island size has been used several times by ecologists to try to explain the differences seen in the taxa richness of pools in close proximity to each other (*Brooks 2004, Oertli et al. 2002, Hall et al. 2004*). This concept, however, does not hold true for all studies previously conducted. For instance, the concept has been shown in

Brooks's (2000) study where larger pools with longer hydroperiods had richer benthic macroinvertebrate diversity, but was not supported by the Hall et al. study (2004). Extrapolating the theory, in a separate study done by Oertli and his colleagues (2002), a set of small sized pools exhibited higher richness than a single large pool of the same total area. Even though a higher diversity occurred in the set of small pools, they were missing certain species that were found in the larger pool. Oertli et al. (2002) also made the prediction that species with larger populations and the ones less tolerant to desiccation may occur in larger pools.

Pool size thus does affect its hydrologic regime/hydroperiod. When ecologists discuss concepts such as island biogeography and that pool size affects diversity, they are indirectly talking about the hydroperiod of that pool. Therefore, I believe it would be correct to assume that the length of a pool's hydroperiod may be a major driving force behind benthic macroinvertebrate community composition and the variability seen in these communities both among pools and over time. This may occur because the number of habitats available as a function of space may be reduced with a shortening of the hydroperiod of the pools (*Lassen 1975, Brooks 2000*). For example, chironomid abundance was highest in shorter hydroperiods whereas amphipod abundance was greater in longer hydroperiod pools (*Brooks 2000*).

However, both physical and chemical factors and not just the length of a pool's hydroperiod may be an influence on macroinvertebrate community structure of pools (*Williams 1997*). For instance, the variability in species occurring in the surrounding tree canopy can influence water chemistry due to the type of litter input, which affects factors such as the release of tannins, thereby affecting the water pH and conductivity. The tree canopy cover will also affect the amount of sunlight reaching a vernal pool, thereby affecting water temperature and dissolved oxygen concentration (*Colburn 2004*). This is further supported by a study conducted in seasonal woodland pools in Minnesota, where macroinvertebrate taxa richness and diversity increased as hydroperiod lengthened, tree canopies opened, litter input decreased and water pH declined (*Brooks 2000, Batzer et al. 2004*). Therefore, I hypothesize that tree canopy composition could also be considered as a factor that affects species composition of invertebrates in vernal pools.

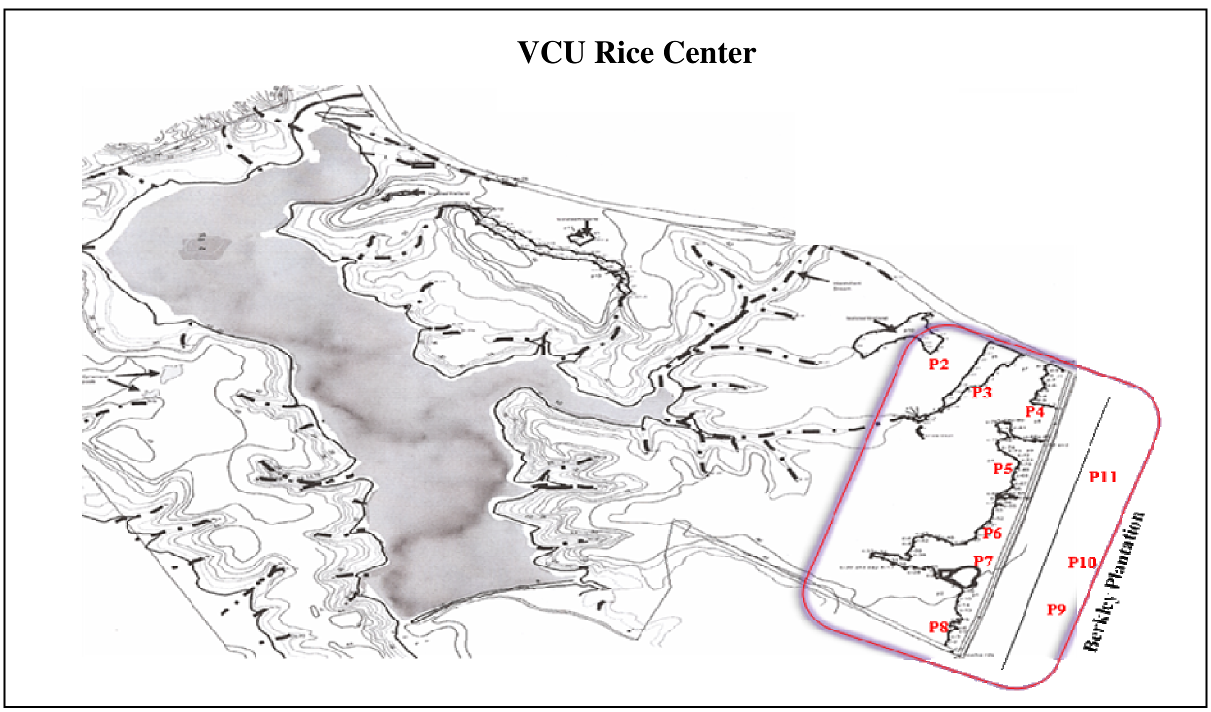
In summation, variables such as tree canopy cover, pool size, and pool depth influence factors such as evapo-transpiration, precipitation runoff into pools, and ground water exchange, which in turn significantly influence a pool's hydroperiod and physiochemical characteristics (*Brooks 2004; Brooks & Hayashi, 2002*). These environmental variables may then have a significant impact on benthic macroinvertebrate community composition in the pools.

Studies regarding how macroinvertebrate communities in vernal pools change with respect to time and space are still very limited, leading to questions concerning their inherent variability and the relationship of environmental variables to that variability. For instance, one view is that vernal pool invertebrates may be habitat generalists (*Batzer et al. 2004*), with another view being that the pool fauna are habitat specialists that have developed adaptations that help them survive the dry phase of the pools (*Kenk 1949, Wiggins et al. 1980, Williams 1987, Williams 1997, Zedler 2003*). However, in previous studies, relationships between macroinvertebrates and environmental variables in vernal pools often were statistically non-significant or at most weakly significant. Hence an effort examining the various relationships among the physical, chemical and biological variables of vernal pools may further the understanding of the structure and functioning of these unique systems.

The primary objective of my study was to determine the extent of variability in the benthic macroinvertebrate communities both spatially and temporally among vernal pools closely situated within a forested landscape. I hypothesized that the macroinvertebrate populations in different pools, though in the same geographic area and watershed, would exhibit significant spatial and temporal differences in community level metrics. I studied how the pool communities changed with respect to species composition, species diversity, species richness and density both among pools and over time (and thus hydroperiod). I also attempted to discern relationships between environmental variables in the pools with variability in their macroinvertebrate communities.

STUDY SITE

There has been little research conducted on the vernal pools of the Virginia coastal plains with respect to macroinvertebrate populations. The VCU Rice Center, a 342 acre field station situated along the lower James River in Charles City County, Virginia, was an obvious choice for such a study given the number and variety of forested vernal pools occurring on site. Ten vernal pools within an area of 20 acres of a loblolly pine forest with a mixed hardwood understory comprised of red maple (*Acer rubrum*), white oak (*Quercus alba*) and sweet gum (*Liquidambar styraciflua*); were chosen for this study. The size of these pools ranged from 15 m^2 to 25 m^2 with changes depending on percent precipitation received. Seven of these pools were located on the Rice Center property and the other three were located on the immediately adjacent Berkeley Plantation properties.



MAP 1: SITE MAP SHOWING LOCATION OF VERNAL POOLS STUDIED (P2 – P11)

MATERIALS & METHODS

MACROINVERTEBRATE SAMPLING:

The first set of winter samples was collected during the months of January and February 2007, with spring samples being collected during April and May 2007. A second set of winter samples was collected in January and February 2008. However, due to the previous year being a very dry year, only five out of the ten previously sampled pools had water. Collection of a second set of spring samples was not possible due to all pools being dry.

Three replicate macroinvertebrate samples were collected from randomly chosen locations within each of the ten vernal pools during each sampling period. Sampling was conducted using a Hess sampler (area = 0.086 m^2; mesh size = 500 µm). Samples were washed through a sieve (mesh size= 425 µm) and preserved in 70% isopropyl alcohol with Rose Bengal stain. In the laboratory, each sample was washed again through a sieve and macroinvertebrates were removed from the sample under a stereomicroscope. Macroinvertebrates were identified generally to the genus level using taxonomic keys such as Merritt, Cummins & Berg (2004), A Guide to Common Freshwater Invertebrates of North America (*Voshell 2002*) and Pennak's Freshwater Invertebrates of the United States (*Smith 2001*).

ENVIRONMENTAL CONDITIONS:

Various environmental factors were measured to determine whether a relationship existed between those variables and the macroinvertebrate occurring in the pools. Dissolved oxygen concentration, conductivity, pH and water temperature were measured once in each pool during each sampling period using appropriate field meters or kits.

Hydroperiod, or the period during which the pools were inundated, was determined by direct observation.

DATA ANALYSIS:

The primary objective of this study was to determine the extent of spatial and temporal variation in the macroinvertebrate communities among a suite of vernal pools. The first stage of data analysis consisted of a description of community taxonomic composition within the pools over time and included comparisons of species present, density, diversity using Shannon Index (H'), and Pielou's evenness index (*Heip 197*4). The density of organisms in each pool was also calculated as the mean of 3 replicate samples.

To examine the similarity in the presence-absence of taxa among the pools, Sorenson's Quotient of Similarity was calculated as,

$$QS = 2*C/\ (A+B)$$

where A and B are the number of species in samples A and B, respectively, and C is the number of species shared by the two samples. The results were categorized into four similarity groups (Very low similarity: 0-0.25; Low similarity: 0.26-0.50; High similarity: 0.51-0.75; Very high similarity: 0.76-1).

To determine the similarity in the proportional abundance of each taxon among pools and over time, a Proportional Similarity Index was calculated as,

$$PS = \Sigma \min (p_i, \rho_i)$$

where p_i is the observed relative frequency of the 'i'th species, $\rho_i = 1/S$ is the expected relative frequency of the 'i'th species and min (p_i , ρ_i) indicates the minimum of the two values.

Regression and correlation analysis were used to determine the relationship between environmental variables and macroinvertebrate community attributes. In addition, relationships between the assemblages and environmental variables across the pools and over time were explored using ordination and cluster analysis. Ordinations were conducted using principal component analysis in PCORD to illustrate spatial and temporal variation in the pool macroinvertebrate communities. On the basis of species abundance, cluster analysis was performed using Euclidean distance in PCORD.

RESULTS

ENVIRONMENTAL VARIABLES:

The environmental variables that were measured during the different sampling periods varied according to the seasons (Figure 1.1-1.3). Water temperature in the pools increased while dissolved oxygen in most pools decreased from winter to spring. Temperature varied among pools with a range of 5.4°C in winter of 2007 and 6.4°C during spring (Figure 1.1). There existed a significant difference between the temperatures of the pools in winter and spring 2007 ($t = 5.169$; $p>0.05$). Dissolved oxygen varied considerably among the pools during each season, ranging from 1.6 mg/L to 8.5 mg/L during winter 2007 and from 2.0 mg/L to 8.0 mg/L during the following spring (Figure 1.2).

The pH of the pools was consistently acidic and varied among the pools. It ranged from 3.76 to nearly 5.96 in the winter 2007 and from a very acidic 3.5 to 5.79 in the spring (Figure 1.3). The values of pH during the second winter of sampling tended to be lower than during the previous winter. The range in conductivity in the pools was fairly similar among seasons, with lows of 35-38 µS/cm and highs of 52-59 µS/cm (Figure 1.4).

Hydroperiod or the length of time that each pool was inundated ranged from 2.5 to 5 months (Figure 2). Inundation of the pools commenced in January 2007 and all pools were dry by the end of May. Pool 10 had the shortest hydroperiod being dry during the spring sampling in 2007.

BIOLOGICAL VARIABLES:

Thirty-five taxa were collected and identified from the 10 vernal pools over the three sampling periods (see Appendix). Diptera (46%), Coleoptera (14%) and Copepoda (11%) composed the majority of the 35 taxa in the pools. The dipteran family Chironomidae was the greatest contributor to the taxonomic diversity of the pools, both spatially and temporally (Appendix). The copepods *Cyclops* and *Senecella* occurred in most of the pools at all times. The higher order taxonomic groups most abundant in the pools during winter 2007 were Diptera, Copepoda and Ostracoda (Figure 3); though the cladoceran *Daphnia* was the most abundant taxon in Pool 8 at this time (Figure 3). In spring 2007, Diptera was the most abundant higher order taxonomic group in all of the pools except for Pools 3, 7 and 11(Figure 4). Oligochaetes were the most abundant taxon in Pool 3, ostracods in Pool 7, and *Daphnia* in Pool 11. In the winter 2008, Copepoda was the most abundant higher order taxon in Pools 2 and 7 while Diptera was most abundant in Pool 5 (Figure 5). Taxa such as Isopoda, Amphipoda and Collembola, though generally not abundant, occurred in the pools across the seasons.

Macroinvertebrate density and taxonomic richness varied within the pools across the seasons (Figures 6.1-6.2). Both the density and the number of taxa in spring 2007 were lower in most pools than in winter 2007. As hydroperiod progressed, taxonomic richness of the pools decreased (Figures 2 & 6.1). Total taxonomic richness in the pools during the winter 2007 ranged from 9 to 18 taxa, whereas it ranged from 6 to 15 taxa the following spring, excluding Pool 10 that was dry and supported no aquatic macroinvertebrates (Figure 6.1). Macroinvertebrate densities ranged from 318 to 1488 individuals m^{-2} in the winter 2007 and declined to 178 to 1128 individuals' m^{-2} in the spring. Both density (124-779 individuals m^{-2}) and taxonomic richness (5-9 taxa) were lower in those pools that had water during the relatively dry winter 2008 compared to during the preceding winter and spring (Figures 6.1-6.2). Macroinvertebrate diversity declined slightly over the three seasons, the biggest decline occurring for the pools in winter 2008 (Figure 6.3). Five out of 9 pools showed increased evenness from winter to spring (Figure 6.4).

Similarity in species composition and the proportional abundance of taxa in the pools both spatially and temporally were determined using Sorenson's Quotient of Similarity and the Proportional Similarity Index (Table 1.1- 2.2). With respect to presence – absence of taxa during winter and spring 2007, only a few comparisons showed either very low or very high similarity (Table 1.3). Similarity between pools was however higher during winter 2007 than during spring 2007, with considerably more pool to pool comparisons (25) in spring having low (26-50%) to very low (0-25%) similarity than the eight comparisons that fell into these categories during the winter (Table 1.3) . Thirty seven pool to pool comparisons for the winter sampling had high (51-75%) to very high (76-100%) similarity compared to only eleven comparisons falling into these categories during spring 2007. When compared across seasons, thirty two out of the forty six pool to pool comparisons showed low to very low similarity indicating considerable differences in the taxa present between the two seasons (Table 1.3). Only six pool to pool comparisons between seasons showed either very high or very low similarity in taxonomic composition.

Most of the pool to pool comparisons during both the winter and spring 2007 showed low to very low proportional similarity (Table 2.1-2.3) indicating differences in the relative abundances of the different taxa among pools. Relative abundances of the taxa were considerably lower during spring than during winter with only two pool to pool comparisons having high proportional similarity in spring compared to thirteen comparisons in that category during the winter (Table 2.3). When compared across seasons, forty out of the forty five pool to pool comparisons showed low to very low similarity in their proportional abundance (Table 2.3).Thus there was much difference in the relative abundance of the taxa present in the pools between seasons.

The pools were positioned according to the variation and associations in species compositions using two dimension ordination analysis. In winter 2007, Pools 5 and 9 formed one cluster and Pools 6 and 10 formed a second cluster (Figure 7), with these four pools being positioned closely together. Other than these pools however the ordination showed a high level of separation among the other pools in winter 2007, indicating differences in the species present among the pools (Figure 7). PCA identified 3 significant axes that cumulatively explained 90% of the variance in the macroinvertebrate scores from the winter 2007 sample sites (Table 3). Nearly 51% of the variance in the macroinvertebrate scores from the pools sampled in winter 2007 was explained by Axis 1 (Table 3). In the spring, 7 out of the 9 pools clustered together suggesting a similarity in their species composition (Figure 8). During this period, Pools 3 and 11 were distant from this cluster and from each other indicating much difference in the species present in these two pools (Figure 8). PCA identified 3 significant axes that cumulatively explained 93% of the variance in the macroinvertebrate scores from the spring 2007 sample sites (Table 4). About 46% of the variance in the macroinvertebrate scores from the pools sampled in spring 2007 was explained by Axis 1 (Table 4). Overall, the pools were more similar in their species in the spring than in the winter 2007. In the winter 2008, Pools 2, 5 and 7 had a high degree of separation among them indicating low similarity in their species (Figure 9).

Cluster analysis showed that in winter 2007, Pools 5, 6, 9 and 10 clustered together and thus were relatively similar to each other in their species composition (Figure 10). Pools 2 and 4 while clustering together were quite dissimilar to the other pools. Pool 7 showed low similarity with all other pools (Figure 10). In spring 2007, Pools 4, 5, 6, 7, 8 and 9 clustered closely together and thus were relatively similar to each other in species composition (Figure 11). Pools 3 and 11 were very unique in their species compositions and hence were very distant from the rest of the pools (Figure 11). Overall the cluster analyses supported the PCA results.

Pearson's correlation analysis showed that there existed a significant relationship between temperature and total species richness of the pools (Table 5 & Figure 12). However further analysis showed that temperature explained only about 37 % of the variation in species richness of the pools (Figure 12). No significant relationship occurred for dissolved oxygen, pH and conductivity with species richness in the pools.

Discussion

The benthic macroinvertebrate communities of the sampled vernal pools exhibited significant variability both spatially and temporally with respect to their species composition, diversity and density. Most of the pools showed a decrease in species richness, density and diversity from winter to spring of 2007, contradictory to other findings where species richness increased with prolonged inundation. High within-pool diversity (α-diversity) and low among-pool diversity (β-diversity) in winter 2007 was observed; while in spring 2007 pools showed low α-diversity and low β-diversity. PCA ordination and cluster analysis both exhibited similar results in that pools in winter showed higher variability in their species composition as compared to those in spring 2007. This shows that even though these pools were in close proximity, most of them were different from each other with respect to species composition initially in winter and then sharing more species in spring. The richness and diversity of the pools did vary across seasons and hence it was assumed that the variability could be affected due to changing seasons as water temperatures became warmer in spring. Statistical analysis did support this possibility in that there did exist a significant relationship between temperature and species richness in the pools; however there was no significant relationship between dissolved oxygen and species richness of the pools.

The fact that in most of these pools, species richness and diversity were higher in winter than in spring 2007 when temperatures are low, suggests that most of the invertebrate species found in these pools in winter can tolerate low temperatures.

Presence of certain macroinvertebrate species with short life cycles only in winter suggests that these organisms have not only tolerance for low temperatures but have evolved themselves to accommodate the drought period if it occurs earlier than normal. This was supported by studies showing that species such as *Daphnia ephemeralis* develop at low temperatures completing their life cycle before temperatures reached a critical threshold in the spring *(Kenk 1949; Colburn 2004).* Though critical temperature thresholds of these macroinvertebrates are not accurately known, there have been studies that make general assumptions based on a range of temperatures from very cold to very hot. Therefore based on this range, it has been observed that ostracods are inactive at cold temperatures *(Colburn 2004).*However this was not the case in my sites where ostracods were more abundant in winter than in spring 2007 (Appendix). This could mean that variables in addition to temperature could be responsible for the seasonal variations in macroinvertebrate communities. Some macroinvertebrate taxa such as chironomid midge larvae are extremely opportunistic and tolerant of stressful environmental factors such as low dissolved oxygen, low temperature and low pH *(Rogers 1998; Higgins and Merritt 1999)* which could be the reason why they were the most diverse taxa in almost all pools in all the seasons sampled (Appendix). Amphipods, copepods and isopods were more abundant in winter than in spring 2007 (Appendix). This was supported by Golladay et al.'s (1997) finding that the abundance of the mentioned macroinvertebrate groups was reduced as hydroperiod progressed. It should be noted, however that due to 500 µm mesh sampling net was not highly efficient in collecting , likely causing a significant underestimate of the richness, diversity and density of the zooplankton.

In spring 2007, pools 3 and 11 were highly dissimilar in their species composition from the rest of the pools (Figure 10). A likely reason for these pools being so different from the others is their low dissolved oxygen concentrations. Therefore due to low oxygen levels, Pool 3 had a high proportion of oligochaetes and Pool 11, due to much higher oxygen levels, supported a high proportion of *Daphnia* (Figures 1.2 & 5) thereby separating these two pools from the other closely related group of pools. The rest of the pools did not show much variation in their oxygen levels.

In this study it was observed that even though Pool 3 had low oxygen levels over all seasons, it had a high species diversity (Figures 1.2 & 2.3). This instance and the statistical analyses performed during this study supports Batzer et al.'s finding that there is only a weak relationship between certain environmental variables and species richness of the pools (*Batzer et al. 2004, Studinski and Grubbs 2007).*

Batzer and his colleagues suggested that vernal pool macroinvertebrates were habitat generalists (2004). The macroinvertebrates present in the pools already have adaptations to compensate for adverse conditions such as low oxygen levels, low temperatures and drought periods, and hence show low or no variation with respect to slight changes happening in the pools. For instance, certain chironomid midge larvae and oligochaetes possess hemoglobin in their blood which helps them to capture oxygen (*Rogers 1998, Sharitz and Batzer 1999 and Colburn 2004).* Certain other macroinvertebrate species such as *Eristalis tenax* (rat tailed maggots) have developed a long siphon that they extend above water surface to breathe *(Sharitz and Batzer 1999).* Some beetle species have air sacs to help them store oxygen *(Colburn 2004)*. The pH of a pool increases as the pools dry, which could also be one of the reasons why some macroinvertebrates tend to complete their life cycle earlier in the season *(Colburn 2004).* These pools are typically rich in wood debris and hence show abundance in macroinvertebrate species such as *Xylotopus* and *Anchytarsus bicolor*, which are wood eating organisms.

When one tries to compare different types of temporary pools to each other, it becomes difficult to describe these systems with respect to their water quality and species composition. Factors such as sources of water, substrate characteristics and the surrounding vegetation, make the water quality characteristics of the pools highly variable and hence support species tolerant of those characteristics. For instance, temporary pools in Oxfordshire, UK, had a slightly alkaline pH (pH= 5.9-8.9) and hence supported invertebrates that were tolerant of alkaline pH *(Collinson et al. 1995);* whereas my study sites had a fairly acidic pH (pH= 3.5-5.8). As another example, the pools studied in southern Michigan had alkaline pH, its alkalinity increasing as the pools shrunk *(Higgins and Merritt 1999)*. In northern Minnesota, vernal pools studied had a mean pH of 6.5 and a mean conductivity of 83 µS/cm *(Batzer et al. 2004)*; whereas my sites had a mean conductivity of 43 µS/cm. The assemblage compositions of these pools depend greatly on their specific regional characteristics. Added to the fact that vernal pools have just started gaining recognition and were not studied much earlier, comparisons between diversities of these regionally different pools becomes difficult.

Larger more permanent systems have been studied longer than vernal pools, hence comparing the differences in their characteristics becomes much easier. The variability observed in the vernal pools is considerably different from what is seen in permanent systems. For example, in vernal pools, macroinvertebrates tend to have not as much permanent bodies of water and thus they divert more of their energy into completing their life cycle in a specified time period. In more permanent water systems where the rate of predation and competition is higher, macroinvertebrates put more energy into anti-predation mechanisms or behavior while simultaneously competing for resources and completing their life cycles. Due to vernal pools being smaller systems than streams or most marshes, the number of habitats and the carrying capacity of the pools tend to be considerably smaller than other larger systems, lending credibility to the biogeographical theory that larger areas support more species (*Oertli et al. 2002).* A higher percentage of shredders are found in streams and rivers than in vernal pools. This is because leaves in flowing systems have more time to get conditioned than leaves in vernal pools (shorter wet periods) making the leaves in flowing systems more palatable. Factors such as these could be why variability in vernal pools is lower than in larger systems *(Colburn 2001, Oertli et al. 2002).*

Virginia has lost 42 % of its wetlands since the 1780's thereby losing a significant fraction of its biodiversity. Vernal pools due to their inconspicuousness during their dry phase become very difficult to delineate and often get destroyed by anthropogenic factors such as dredging, mining and construction. These losses however are almost never recorded because according to the US Supreme Court, isolated wetlands are not 'waters of United States'. It could be inferred that the recorded wetland loss stated above did not include many of the isolated wetlands such as vernal pools that were truly lost. The variability in vernal pools if studied extensively will help in understanding several concepts that are still unclear. Due to their smaller size, vernal pools would be ideal study sites for extrapolating concepts onto larger systems. Vernal pools are unique wetlands supporting a small yet important proportion of biodiversity. Efforts need to be made to understand, preserve and manage these systems.

TABLE 1.1: SIMILARITY COEFFICIENTS CALCULATED USING SORENSON'S QUOTIENT OF SIMILARITY, TO DETERMINE THE SIMILARITIES IN PRESENCE AND ABSENCE OF SPECIES AMONG POOLS SAMPLED WITHIN THE SAME SEASON (WINTER AND SPRING 2007). THE BOLD NUMBERS INDICATE THE POOLS WITH LOWEST AND HIGHEST SIMILARITIES.

					SPRING 2007					
	Pool 2	**Pool 3**	**Pool 4**	**Pool 5**	**Pool 6**	**Pool 7**	**Pool 8**	**Pool 9**	**Pool 10**	**Pool 11**
Pool 2	--	0.38	0.46	0.43	0.46	0.36	0.53	0.40	--	0.42
Pool 3	0.71	--	0.63	0.30	0.42	**0.12**	0.38	0.63	--	0.32
Pool 4	0.67	0.69	--	0.47	0.38	0.29	0.67	0.62	--	0.55
Pool 5	0.40	0.56	**0.32**	--	0.47	0.67	0.42	**0.14**	--	0.52
Pool 6	0.42	0.69	0.70	0.64	--	**0.14**	0.56	0.31	--	0.64
Pool 7	0.42	0.55	0.52	0.55	0.54	--	0.38	**0.00**	--	**0.20**
Pool 8	0.54	0.71	0.64	0.50	0.71	0.71	--	0.40	--	0.67
Pool 9	0.67	0.63	0.54	0.48	0.62	0.55	0.58	--	--	0.32
Pool 10	0.67	**0.76**	**0.78**	0.46	**0.85**	0.62	0.71	**0.76**	--	**0.00**
Pool 11	0.48	0.71	0.57	0.59	0.71	0.65	0.67	0.65	0.71	--
			WINTER 2007							

TABLE 1.2: SIMILARITY COEFFICIENTS CALCULATED USING SORENSON'S QUOTIENT OF SIMILARITY TO DETERMINE THE SIMILARITY IN TAXONOMIC COMPOSITION BETWEEN POOLS SAMPLED IN WINTER VERSUS SPRING 2007.POND 10 WAS DRY DURING THIS SAMPLING AND THUS IS NOT INCLUDED IN THE TABLE. THE BOLD NUMBERS INDICATE THE POOLS WITH LOWEST AND HIGHEST SIMILARITIES.

	Pool 2	**Pool 3**	**Pool 4**	**Pool 5**	**Pool 6**	**Pool 7**	**Pool 8**	**Pool 9**	**Pool 10**	**Pool 11**
Pool 2	**0.24**									
Pool 3	**0.27**	0.37								
Pool 4	0.50	0.64	0.63							
Pool 5	0.48	0.54	0.60	**0.21**						
Pool 6	**0.20**	0.32	0.32	**0.22**	0.36					
Pool 7	0.44	0.44	0.35	**0.13**	0.40	0.40				
Pool 8	0.55	0.59	0.57	0.50	0.50	**0.75**	**0.77**			
Pool 9	0.35	0.36	0.38	0.40	0.42	0.32	0.38	0.36		
Pool 11	0.39	0.58	0.56	0.50	0.50	0.64	0.67	0.45	0.50	0.56

TABLE 1.3: SIMILARITY IN THE PRESENCE-ABSENCE OF TAXA AMONG POOLS DURING THE WINTER AND SPRING 2007 AND BETWEEN THOSE TWO SEASONS CALCULATED USING SORENSON'S QUOTIENT OF SIMILARITY. NUMBERS OF COMPARISONS FALLING INTO SIMILARITY CATEGORIES IS SHOWN BELOW. CATEGORIES ARE DEFINED AS: VERY LOW SIMILARITY: 0-0.25; LOW SIMILARITY: 0.26-0.50; HIGH SIMILARITY: 0.51-0.75; VERY HIGH SIMILARITY: 0.76-1.

	Winter 2007	**Spring 2007**	**Winter vs. Spring**
Very Low Similarity	0	5	5
Low Similarity	8	20	27
High Similarity	33	11	13
Very High Similarity	4	0	1

TABLE 2.1: PROPORTIONAL SIMILARITY INDICES DETERMINING THE SIMILARITIES IN THE RELATIVE ABUNDANCE OF SPECIES AMONG POOLS SAMPLED WITHIN THE SAME SEASON (WINTER AND SPRING 2007). THE BOLD NUMBERS INDICATE THE POOLS WITH LOWEST AND HIGHEST SIMILARITIES.

Spring 2007										
	Pool 2	**Pool 3**	**Pool 4**	**Pool 5**	**Pool 6**	**Pool 7**	**Pool 8**	**Pool 9**	**Pool 10**	**Pool 11**
Pool 2	--	22	31	32	59	5	26	39	--	25
Pool 3	51	--	42	21	21	6	31	41	--	21
Pool 4	57	70	--	38	30	24	57	46	--	28
Pool 5	35	38	39	--	62	16	40	27	--	38
Pool 6	49	66	65	40	--	1	37	35	--	41
Pool 7	9	21	22	18	30	--	9	0	--	2
Pool 8	24	42	35	10	36	39	--	36	--	39
Pool 9	33	53	38	40	42	12	20	--	--	3
Pool 10	51	64	56	44	61	25	42	55	--	22
Pool 11	21	38	35	34	53	55	36	30	37	--
Winter 2007										

TABLE 2.2: PROPORTIONAL SIMILARITY INDICES DETERMINING THE SIMILARITIES THE RELATIVE ABUNDANCE OF SPECIES AMONG POOLS SAMPLED BETWEEN SEASONS (WINTER VS SPRING 2007). THE BOLD NUMBERS INDICATE THE POOLS WITH LOWEST AND HIGHEST SIMILARITIES.

	Pool 2	**Pool 3**	**Pool 4**	**Pool 5**	**Pool 6**	**Pool 7**	**Pool 8**	**Pool 9**	**Pool 10**	**Pool 11**
Pool 2	45									
Pool 3	12	39								
Pool 4	8	15	26							
Pool 5	38	18	40	99						
Pool 6	39	19	28	52	70					
Pool 7	23	1	10	15	1	32				
Pool 8	18	20	33	25	24	5	32			
Pool 9	19	38	44	21	22	0	51	55		
Pool 11	10	9	12	17	17	1	24	30	10	42

TABLE 2.3: SIMILARITY IN THE PROPORTIONAL ABUNDANCE OF TAXA AMONG POOLS DURING THE WINTER AND SPRING 2007 AND BETWEEN THOSE TWO SEASONS CALCULATED USING THE PROPORTIONAL INDEX OF SIMILARITY. NUMBERS OF COMPARISONS FALLING INTO SIMILARITY CATEGORIES IS SHOWN BELOW. CATEGORIES ARE DEFINED AS: VERY LOW SIMILARITY: 0-25%; LOW SIMILARITY: 26-50%; HIGH SIMILARITY: 51-75%; VERY HIGH SIMILARITY: 76-100%.

	Winter 2007	**Spring 2007**	**Winter vs. Spring**
Very Low Similarity	10	14	26
Low Similarity	22	18	14
High Similarity	13	2	5
Very High Similarity	0	0	0

TABLE 3: EIGENVALUES AND CUMULATIVE PERCENT VARIANCE EXTRACTED FROM THE FIRST THREE ORDINATION AXES FIT TO INVERTEBRATE SCORES FROM POOLS SAMPLED IN WINTER 2007. AXES CONSIDERED SIGNIFICANT WHEN OBSERVED EIGENVALUES EXCEED BROKEN-STICK.

AXIS	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	40804.801	50.880	50.880	9936.723
2	22187.184	27.666	78.546	7506.491
3	9506.020	11.853	90.399	6291.376

TABLE 4: EIGENVALUES AND CUMULATIVE PERCENT VARIANCE EXTRACTED FROM THE FIRST THREE ORDINATION AXES FIT TO INVERTEBRATE SCORES FROM POOLS SAMPLED IN SPRING 2007. AXES CONSIDERED SIGNIFICANT WHEN OBSERVED EIGENVALUES EXCEED BROKEN-STICK.

AXIS	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	24406.973	46.549	46.549	6496.646
2	18036.137	34.398	80.947	4907.757
3	6211.913	11.847	92.794	4113.312

TABLE 5: RESULTS OF ANALYSES USING PEARSON'S CORRELATION AND LINEAR REGRESSION, BETWEEN TOTAL SPECIES RICHNESS, AVERAGE SPECIES RICHNESS AND ENVIRONMENTAL VARIABLES.

Variables	Total Species Richness		Average Species Richness	
	r^2	Pearson's Correlation	r^2	Pearson's Correlation
Dissolved Oxygen	0.11	0.34	0.13	0.36
Temperature	0.37	-0.61**	0.27	-0.52*
pH	0.07	-0.26	0.09	-0.29
Conductivity	0.07	0.27	0.06	0.24

* Correlation is significant at the 0.05 level

** Correlation is significant at the 0.01 level

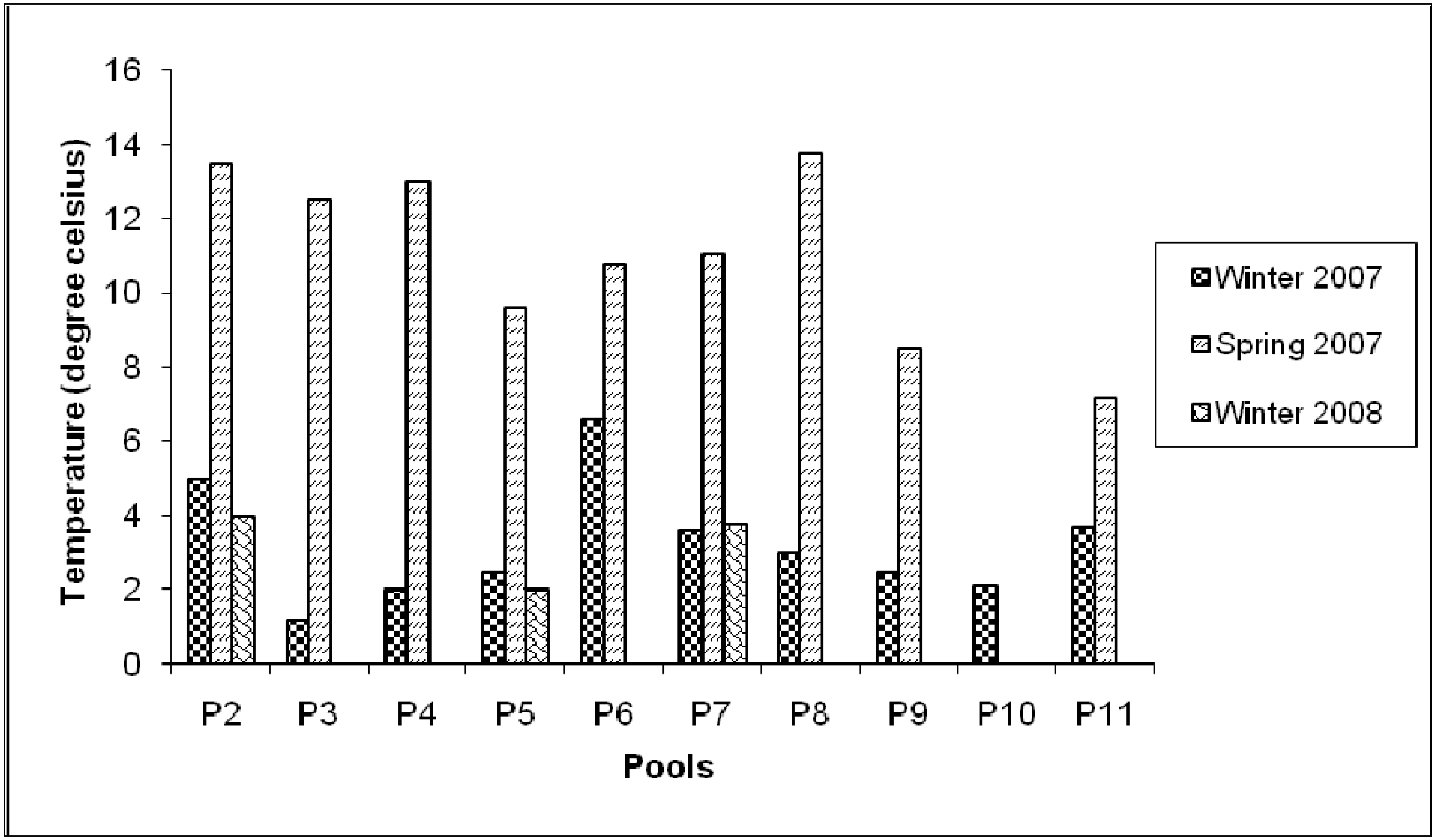


FIGURE 1.1: TEMPERATURE DATA OF THE 10 POOLS SAMPLED IN WINTER AND SPRING OF 2007

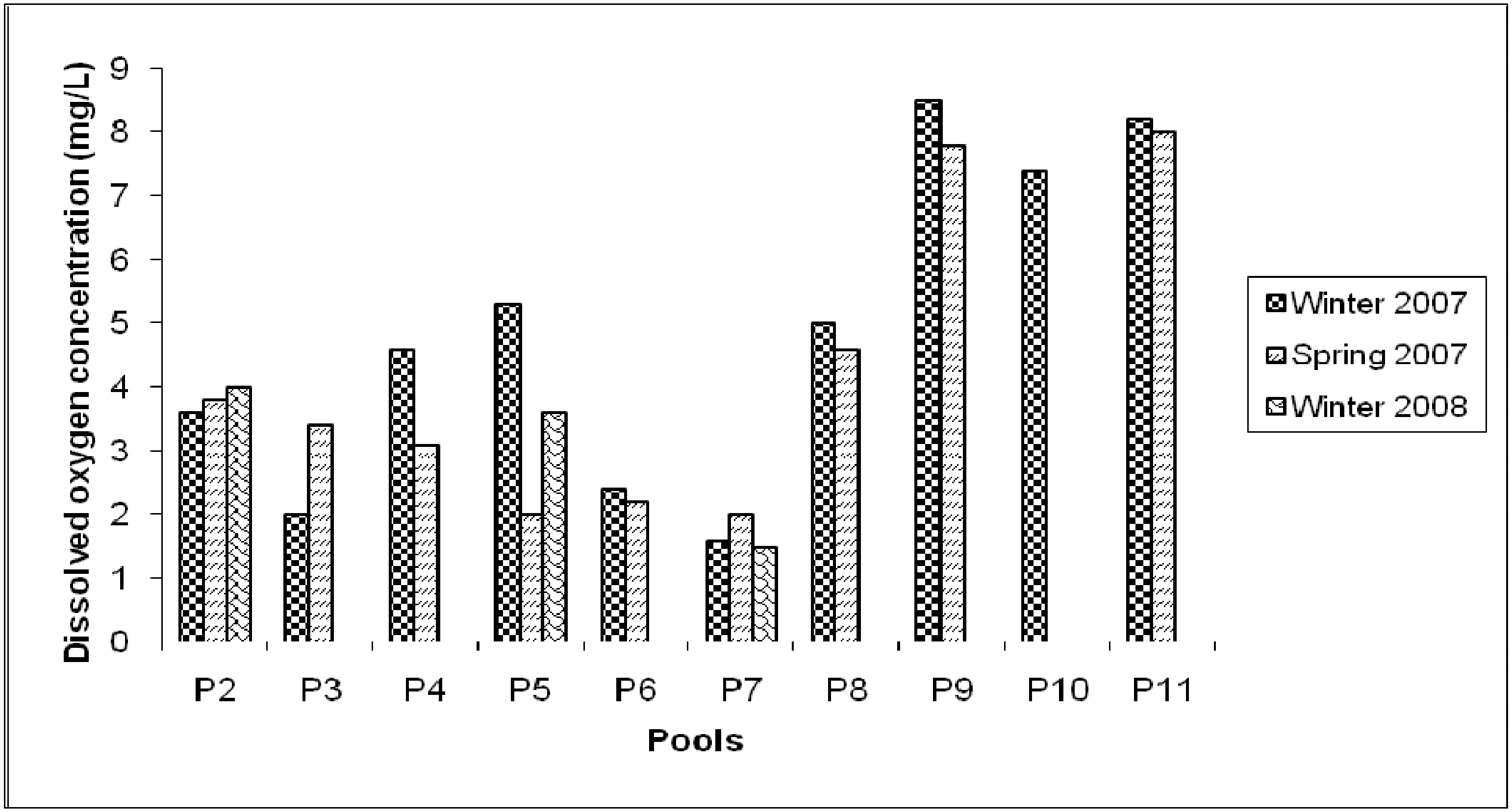


FIGURE 1.2: DISSOLVED OXYGEN DATA OF THE 10 POOLS SAMPLED IN WINTER AND SPRING OF 2007.

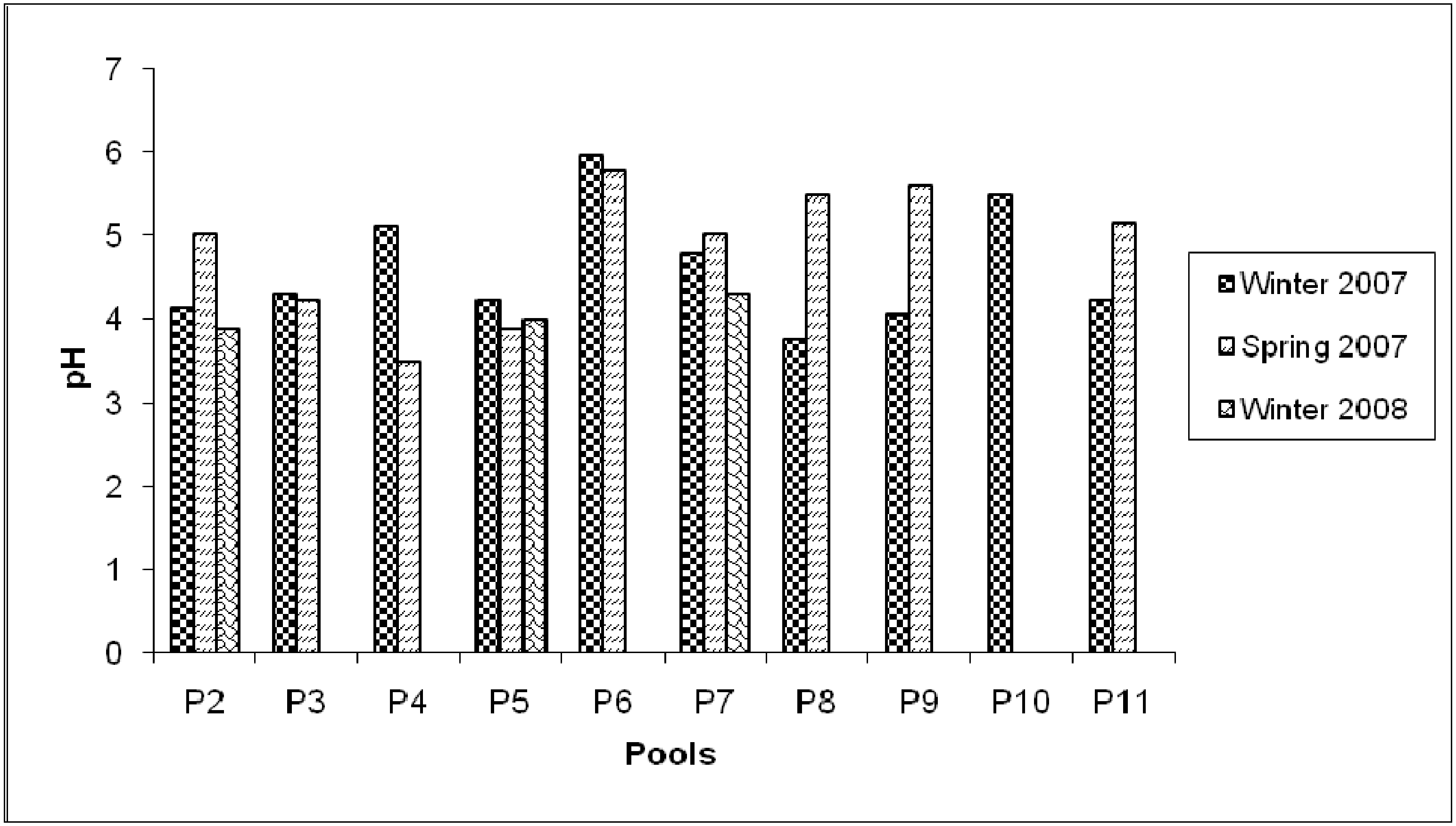


FIGURE 1.3: PH DATA OF THE 10 POOLS SAMPLED IN WINTER AND SPRING OF 2007.

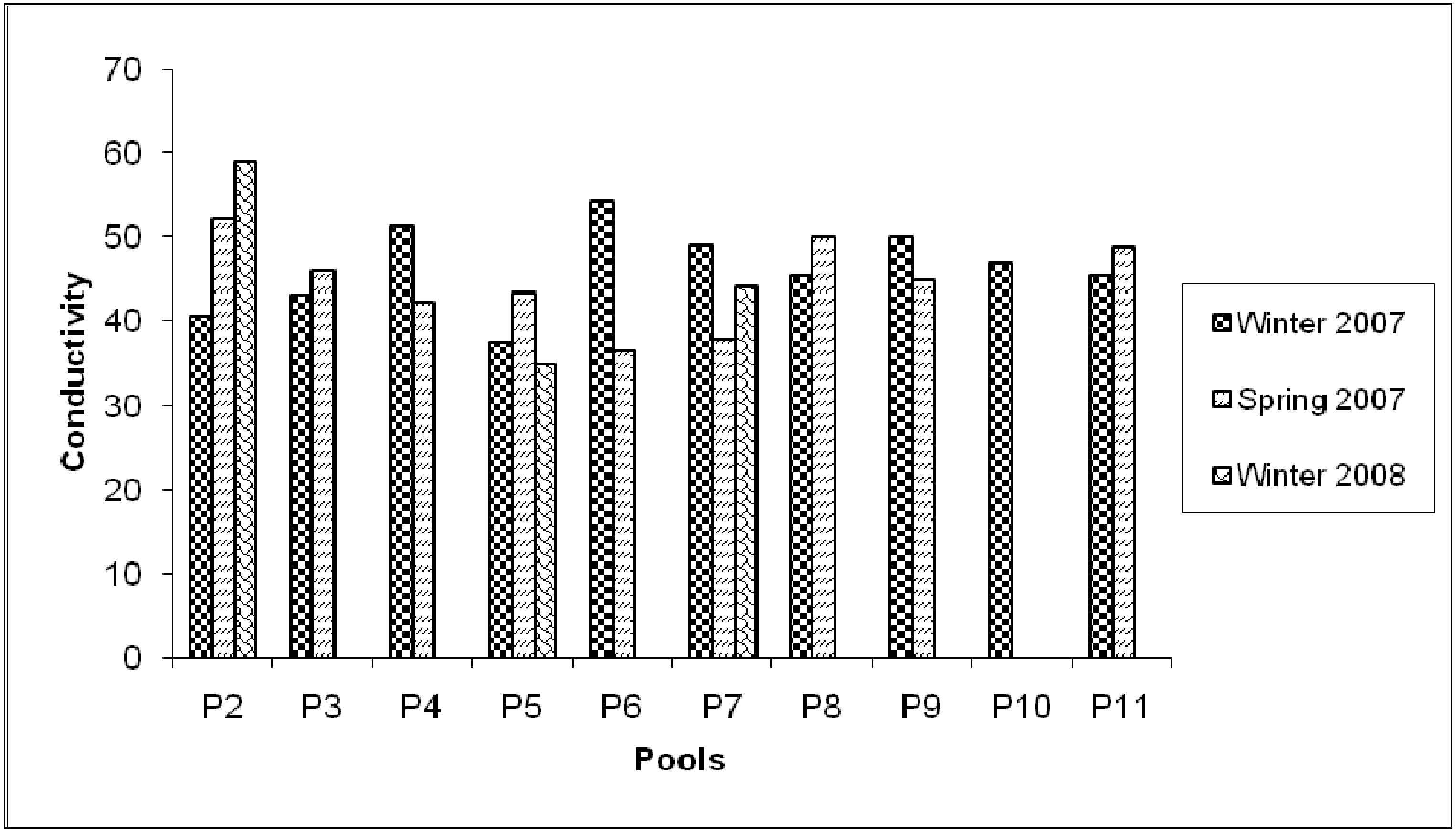


FIGURE 1.4: CONDUCTIVITY DATA OF THE 10 POOLS SAMPLED IN WINTER AND SPRING OF 2007.

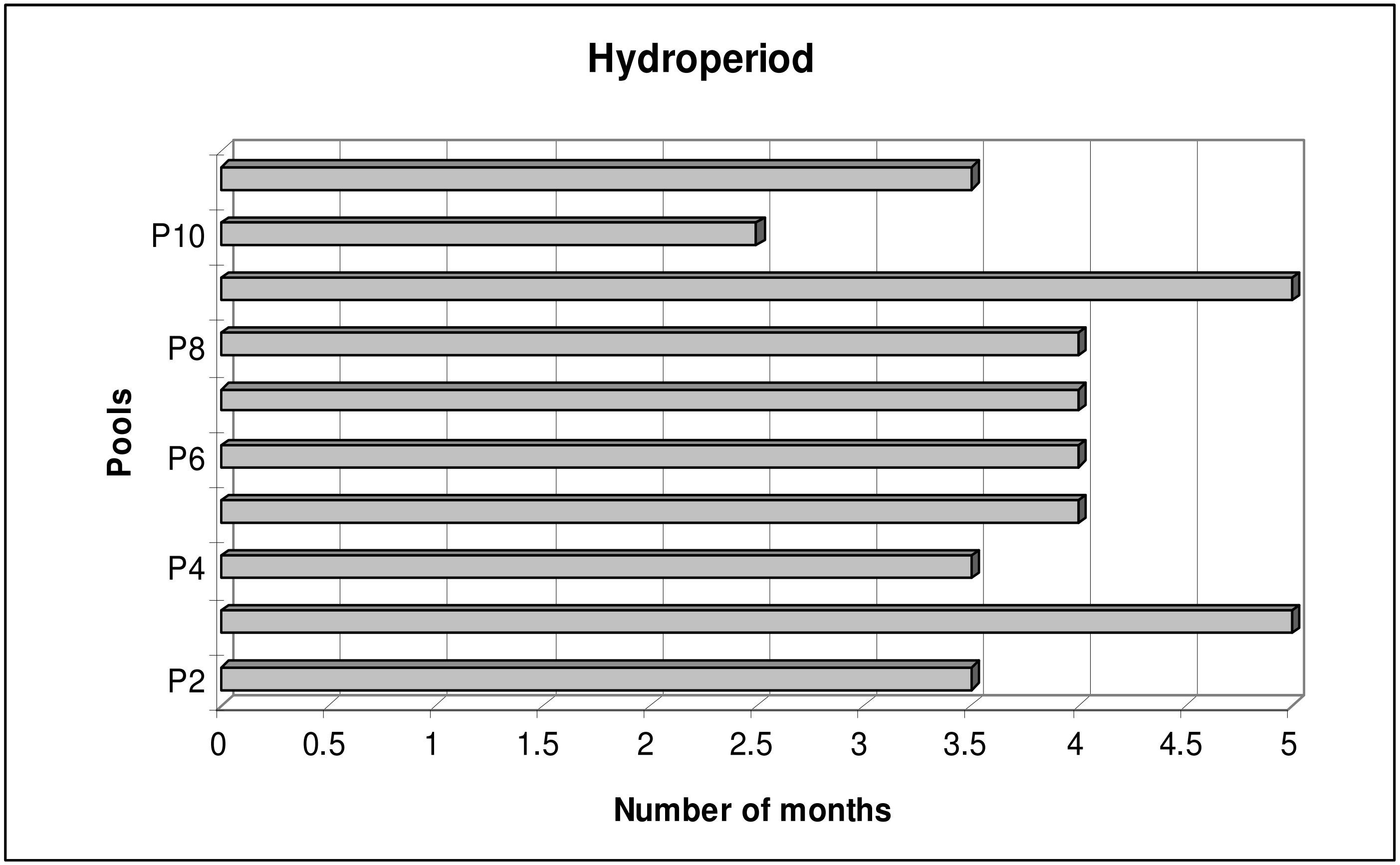


FIGURE 2: HYDROPERIOD IN TERMS OF THE NUMBER OF MONTHS THE POOLS WERE INUNDATED, WITH MONTH 0 BEING JANUARY AND MONTH 5 BEING MAY 2007.

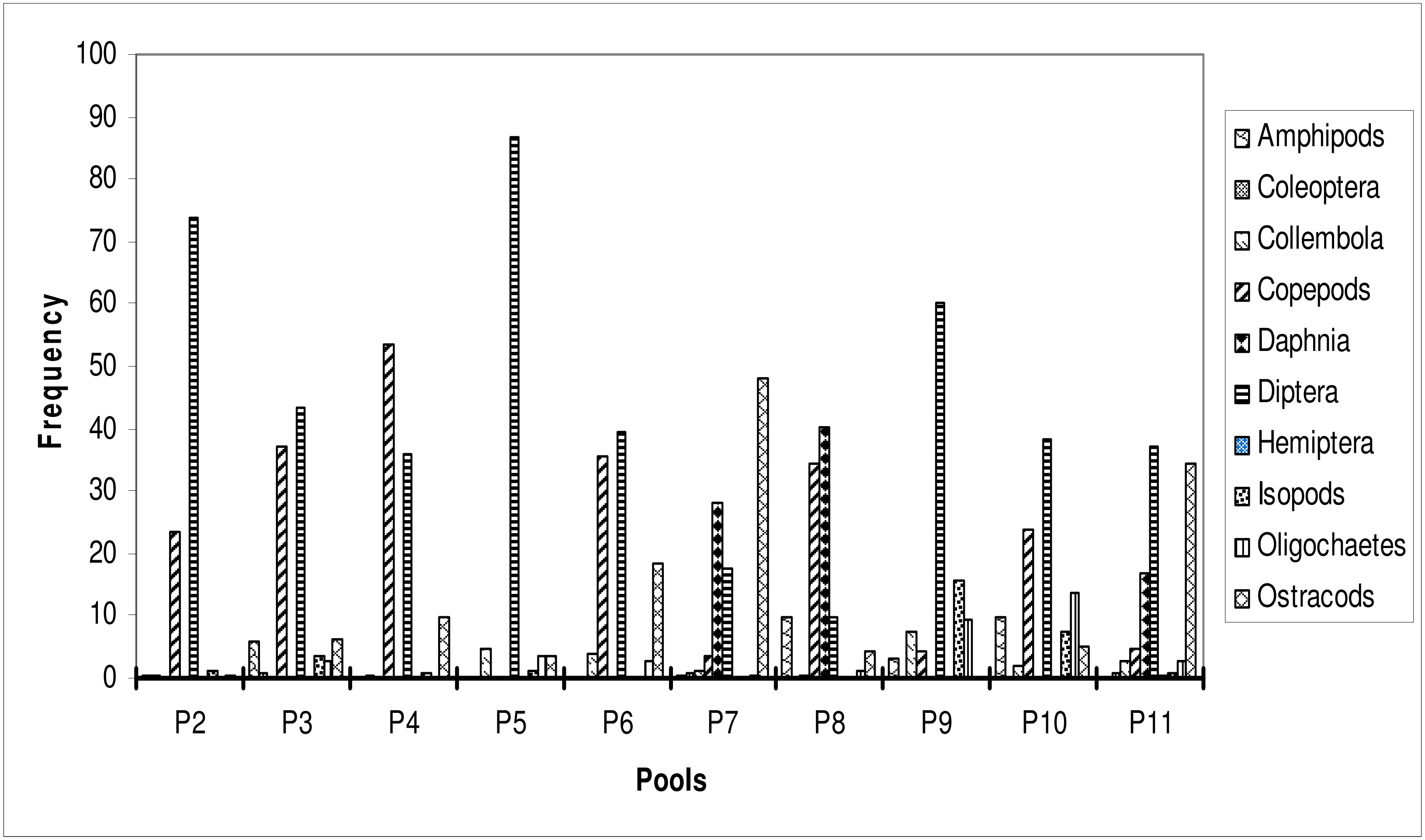


FIGURE 3: PERCENTAGE WISE DISTRIBUTION OF MACROINVERTEBRATE TAXA GROUPS WITHIN THE POOLS IN WINTER 2007.

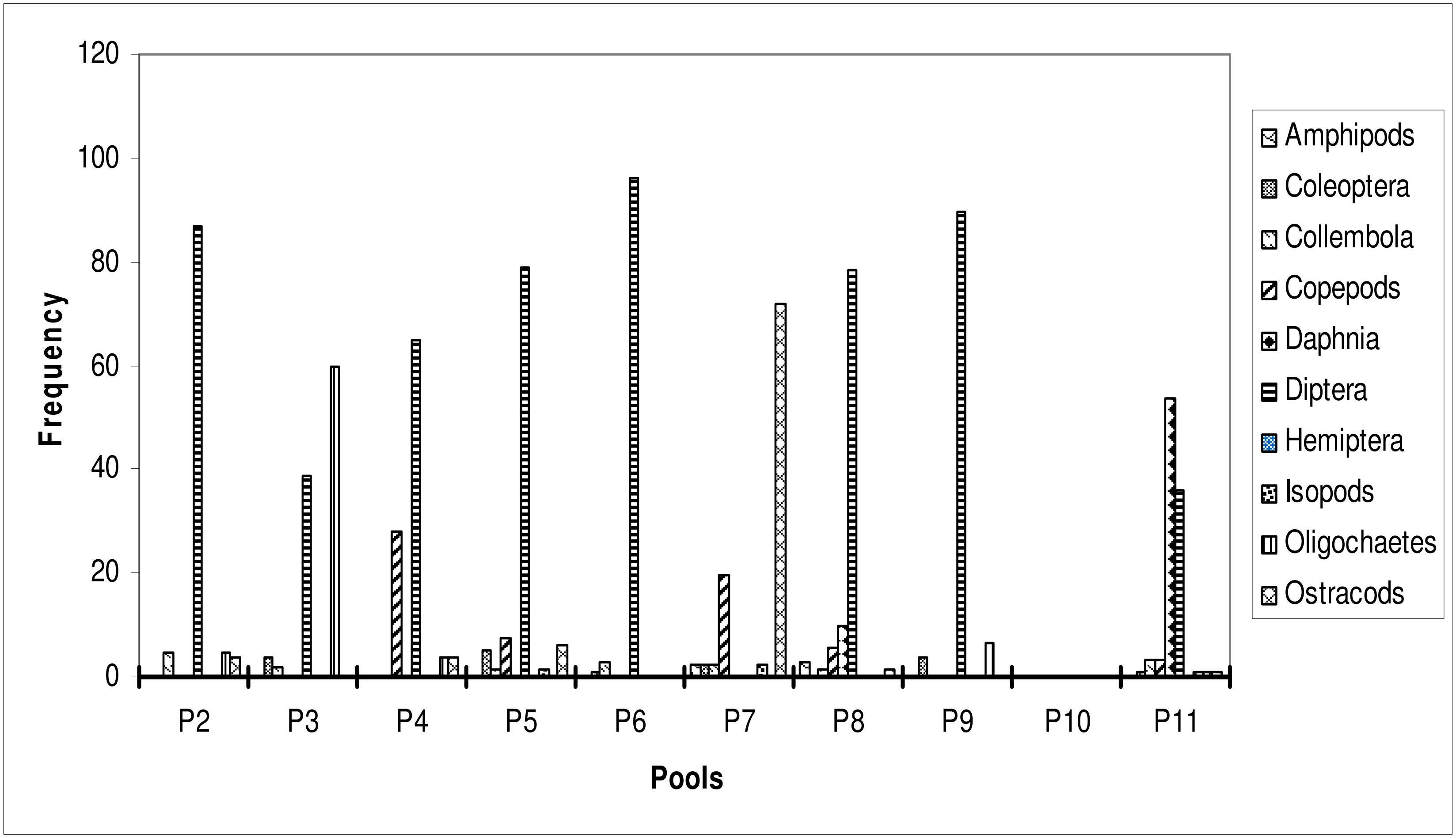


FIGURE 4: PERCENTAGE WISE DISTRIBUTION OF MACROINVERTEBRATE TAXA GROUPS WITHIN THE POOLS IN SPRING 2007.

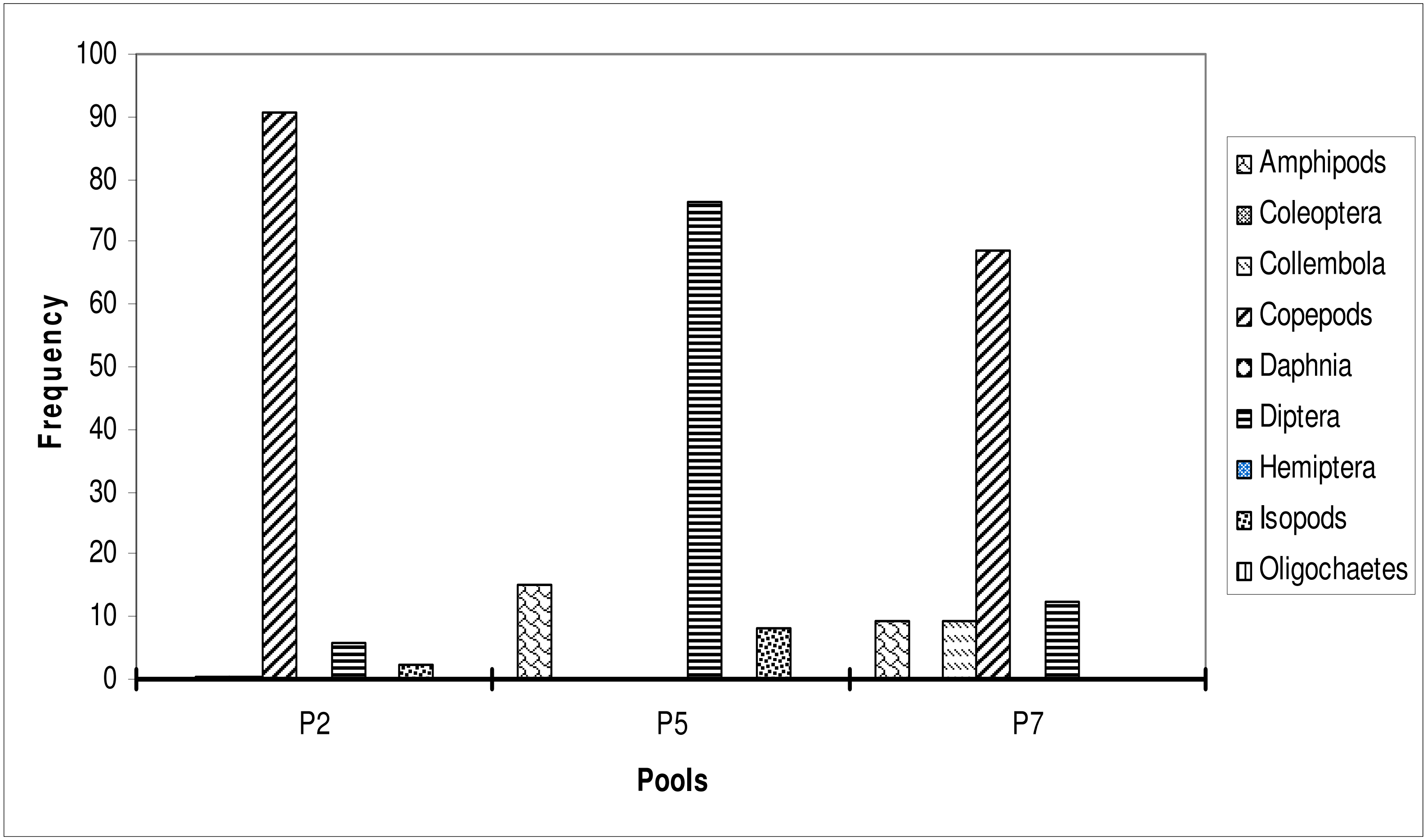


FIGURE 5: PERCENTAGE WISE DISTRIBUTION OF MACROINVERTEBRATE TAXA GROUPS WITHIN THE POOLS IN WINTER 2008.

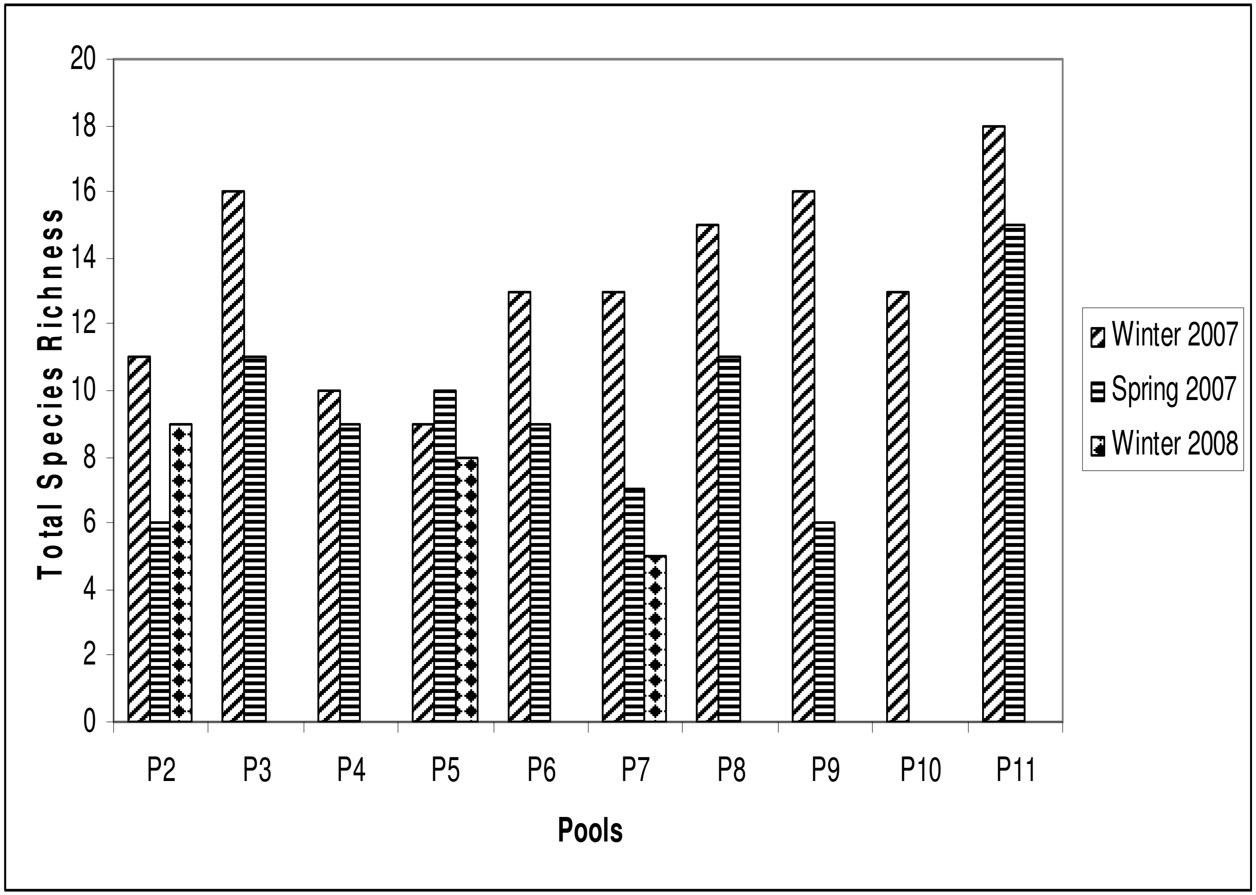


FIGURE 6.1: TOTAL SPECIES RICHNESS IS THE NUMBER OF TAXA OCCURRING IN THE THREE REPLICATE SAMPLES COMBINED FOR THE MACROINVERTEBRATE COMMUNITIES OF THE 10 POOLS SAMPLED IN ALL SEASONS.

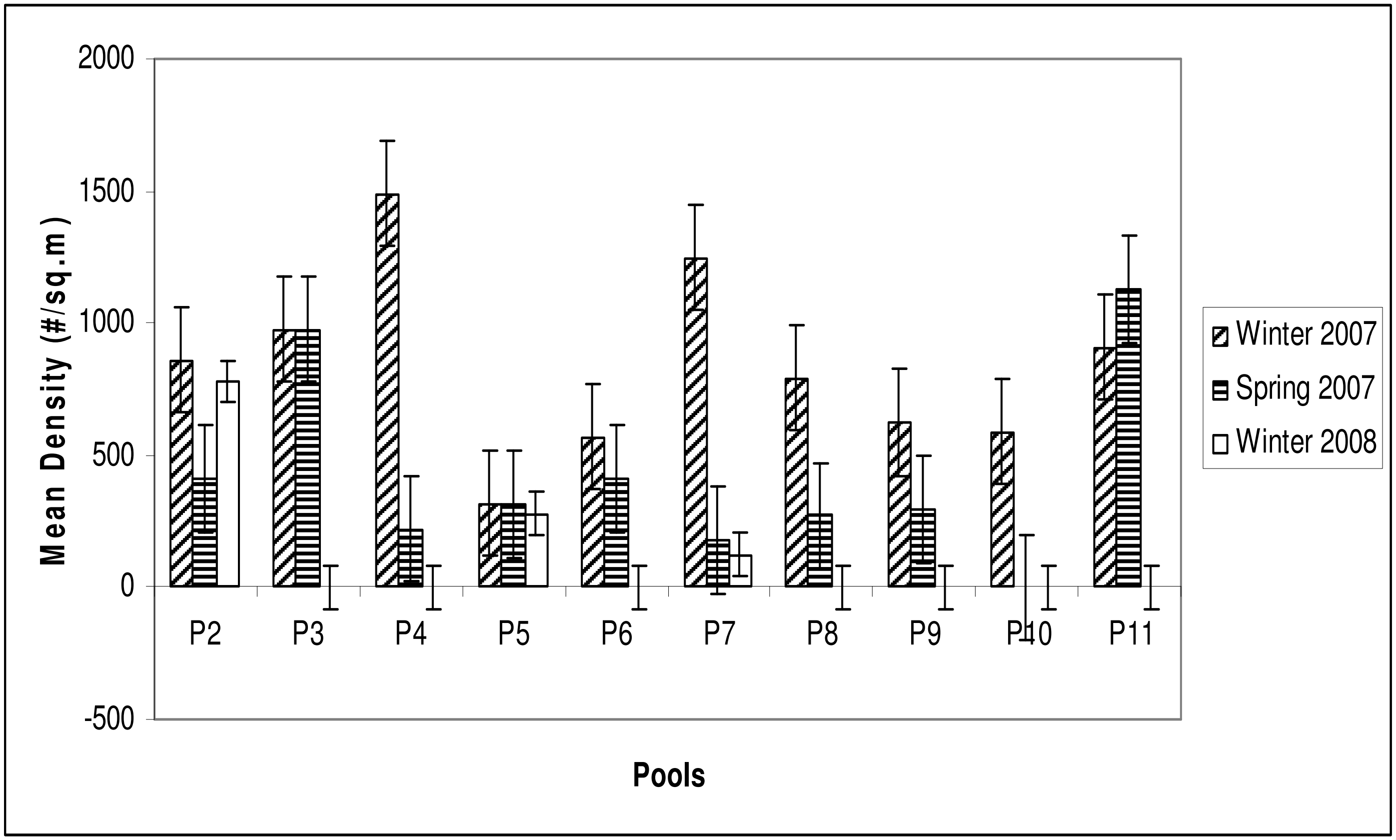


FIGURE 6.2: MEAN DENSITY OF THE MACROINVERTEBRATE COMMUNITIES OF THE 10 POOLS SAMPLED IN ALL SEASONS.

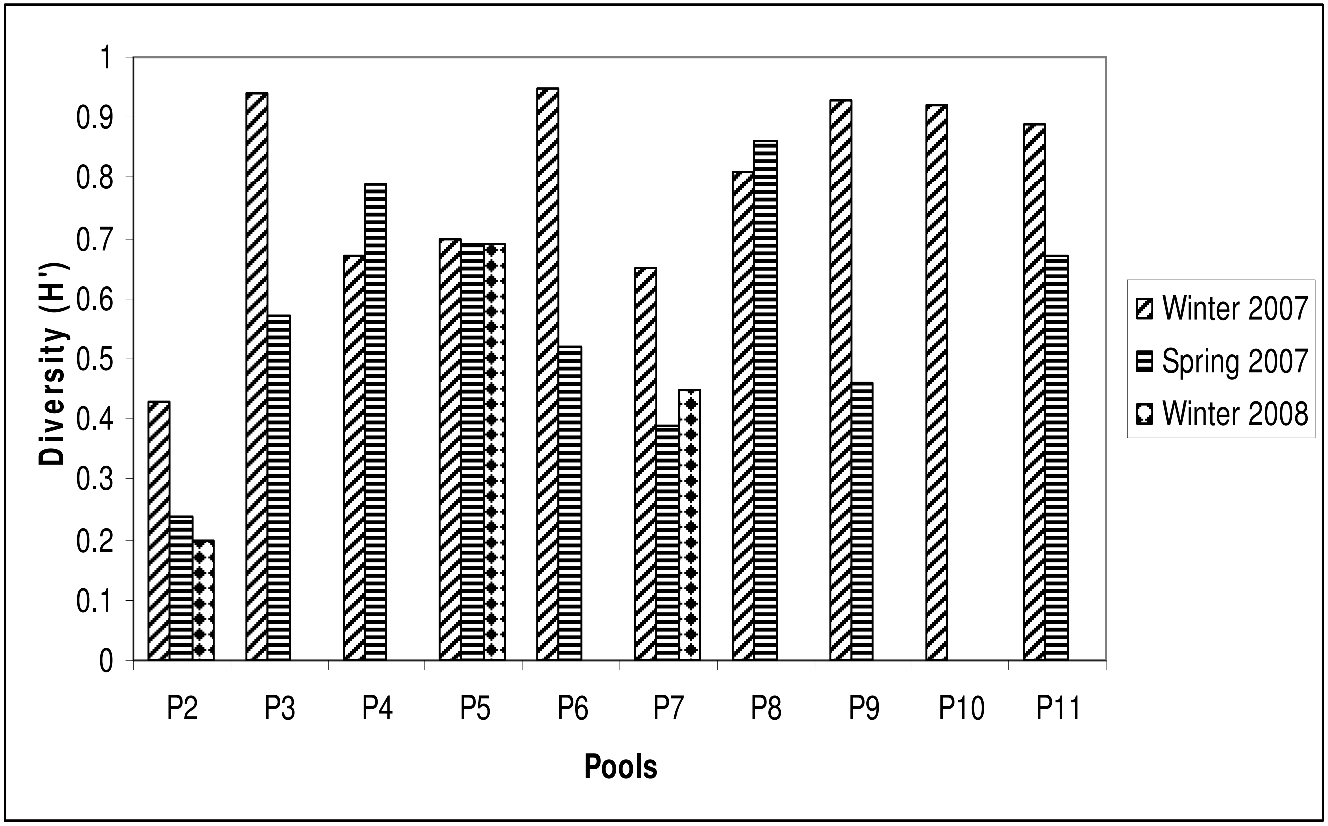


FIGURE 6.3: SHANNON –WEINER DIVERSITY INDEX (H) FOR THE MACROINVERTEBRATE COMMUNITIES OF THE 10 POOLS SAMPLED IN ALL SEASONS SAMPLED.

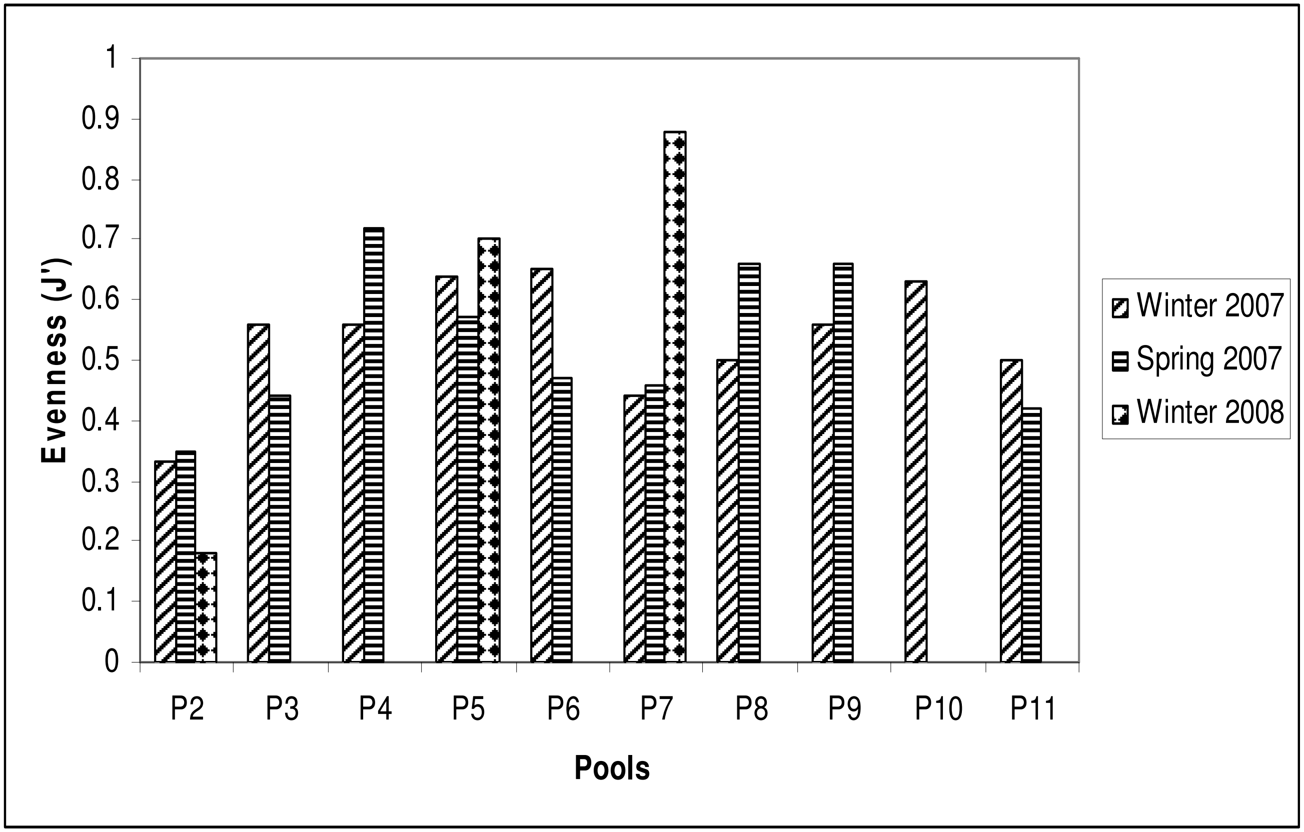


FIGURE 6.4: PIELOU'S EVENNESS (J') OF THE MACROINVERTEBRATE COMMUNITIES OF THE 10 POOLS SAMPLED IN ALL SEASONS.

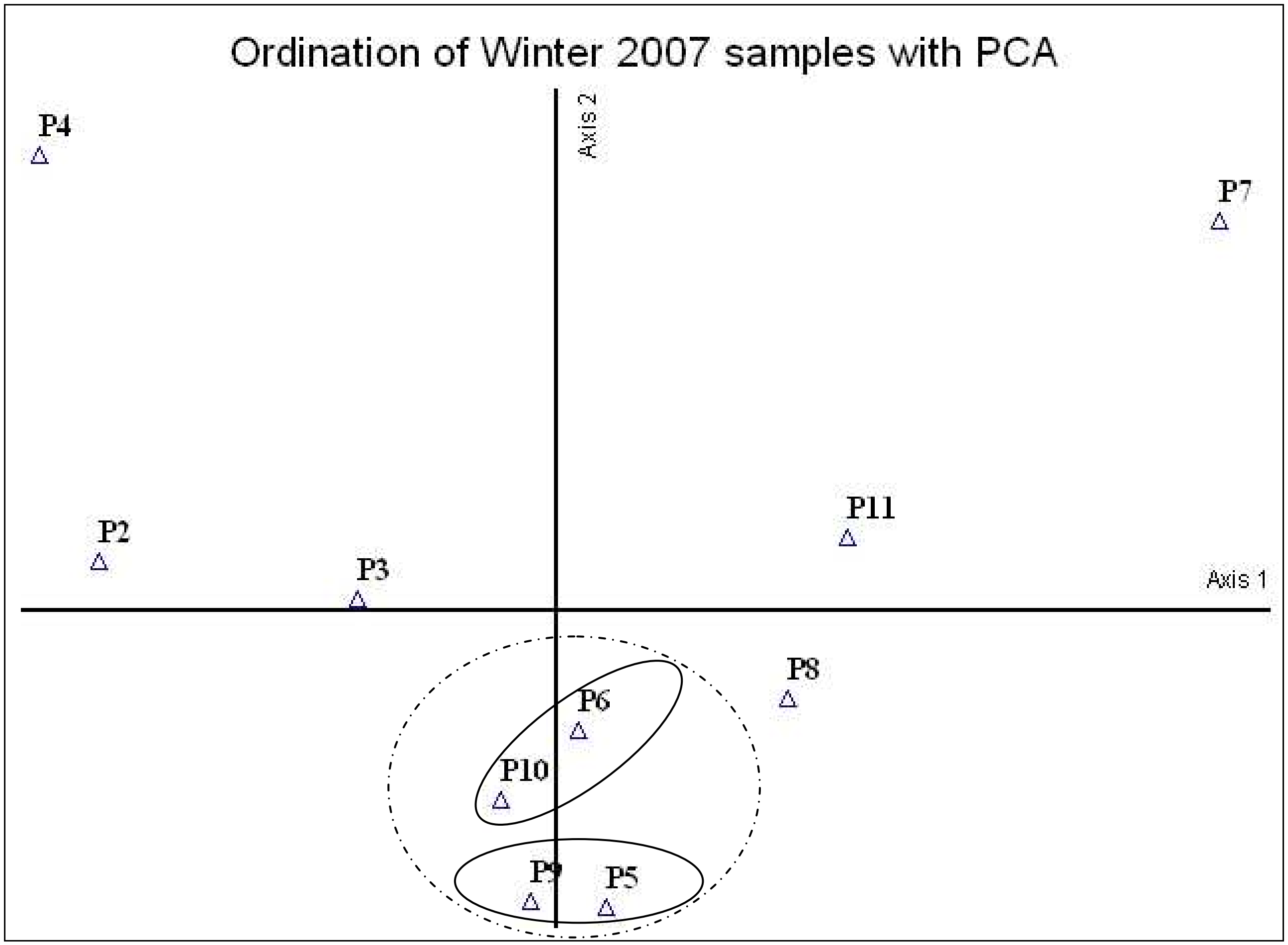


FIGURE 7: A TWO DIMENSIONAL ORDINATION OF POOLS SAMPLED IN WINTER 2007, IN SPECIES SPACE. DISTANCES BETWEEN POOLS APPROXIMATE DISSIMILARITY BETWEEN POOLS WITH RESPECT TO THEIR RESPECTIVE SPECIES.

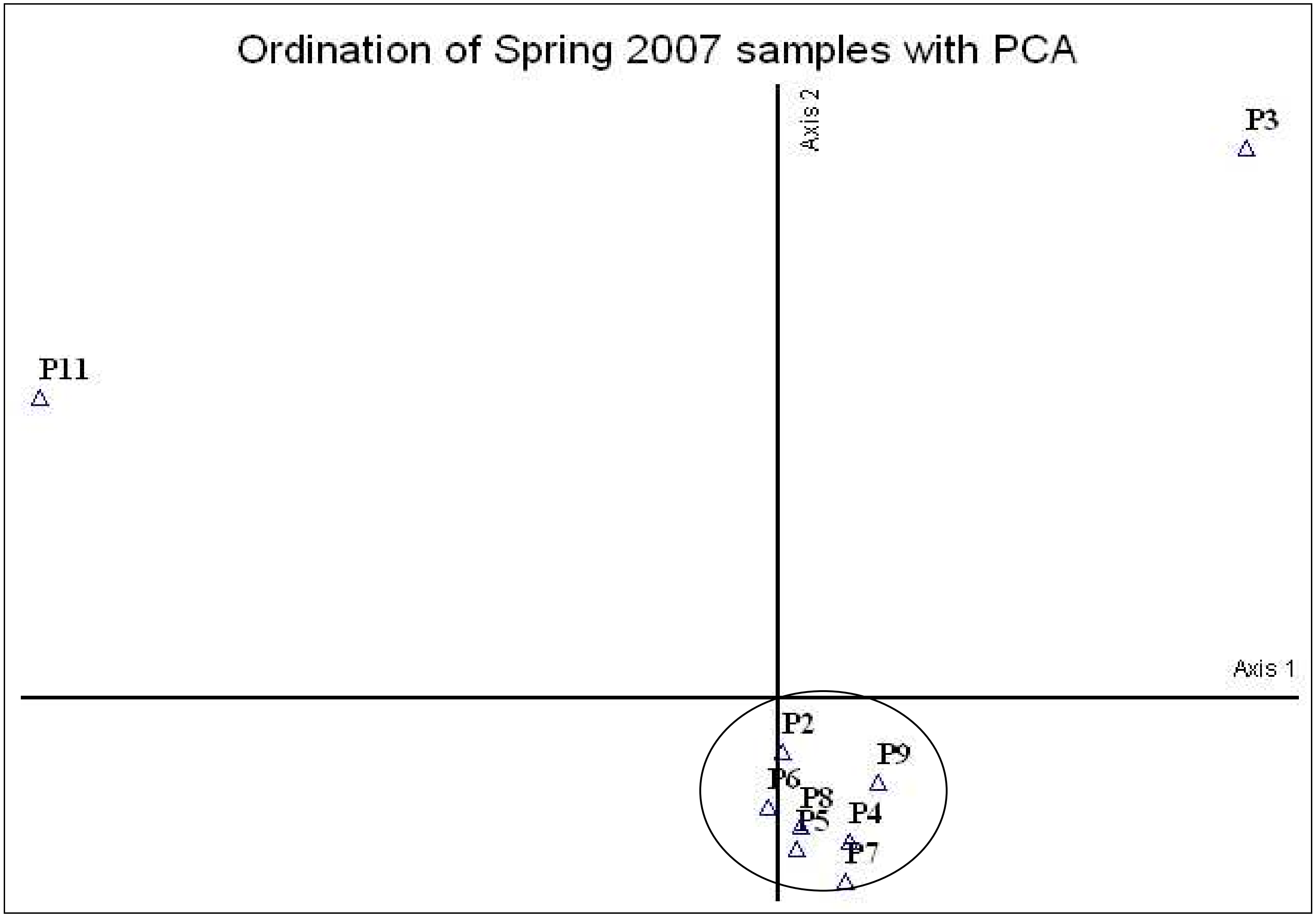


FIGURE 8: A TWO DIMENSIONAL ORDINATION OF POOLS SAMPLED IN SPRING 2007, IN SPECIES SPACE. DISTANCES BETWEEN POOLS APPROXIMATE DISSIMILARITY BETWEEN POOLS WITH RESPECT TO THEIR SPECIES COMPOSITION.

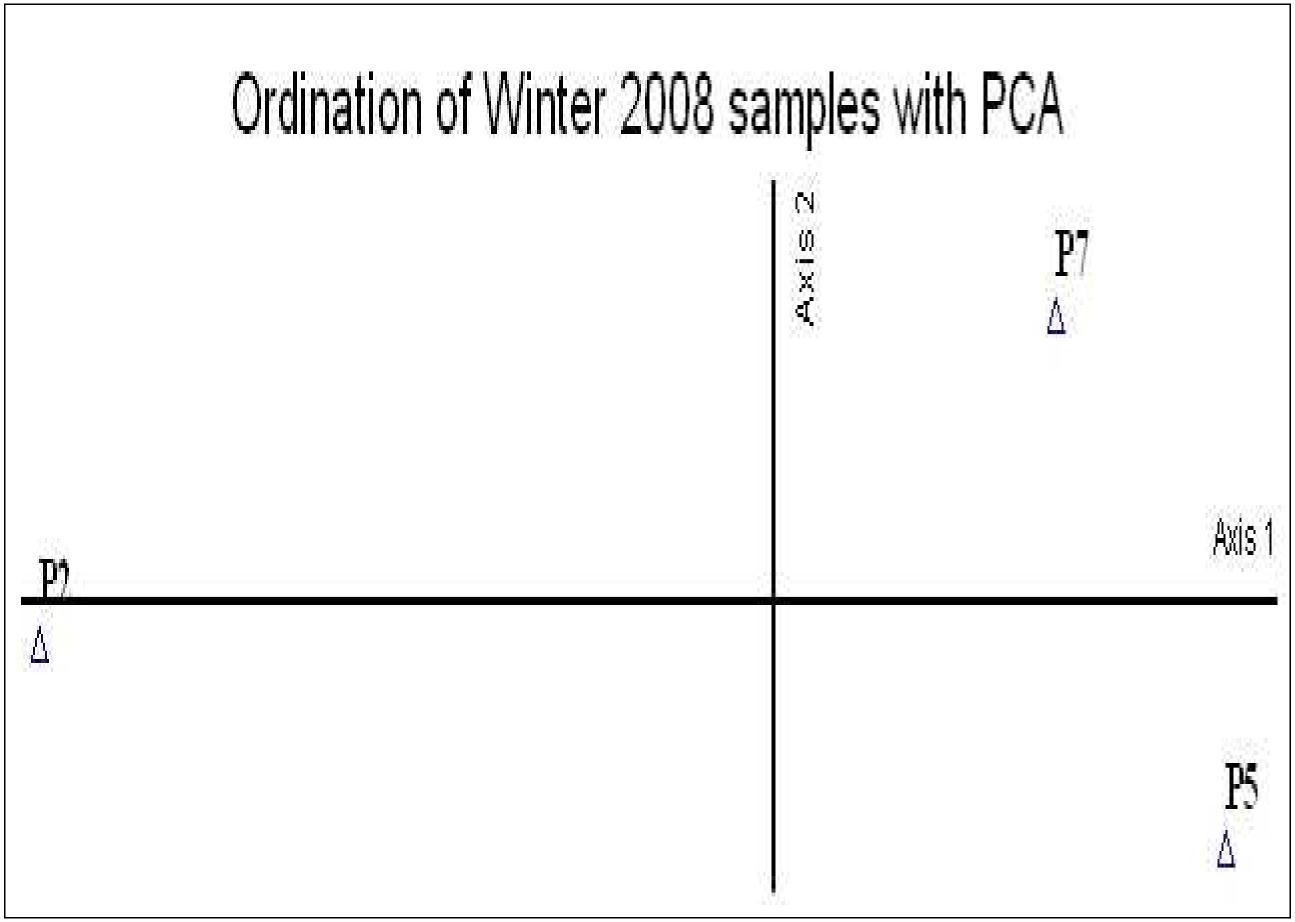


FIGURE 9: A TWO DIMENSIONAL ORDINATION OF POOLS SAMPLED IN WINTER 2008, IN SPECIES SPACE. DISTANCES BETWEEN POOLS APPROXIMATE DISSIMILARITY BETWEEN POOLS WITH RESPECT TO THEIR SPECIES COMPOSITION.

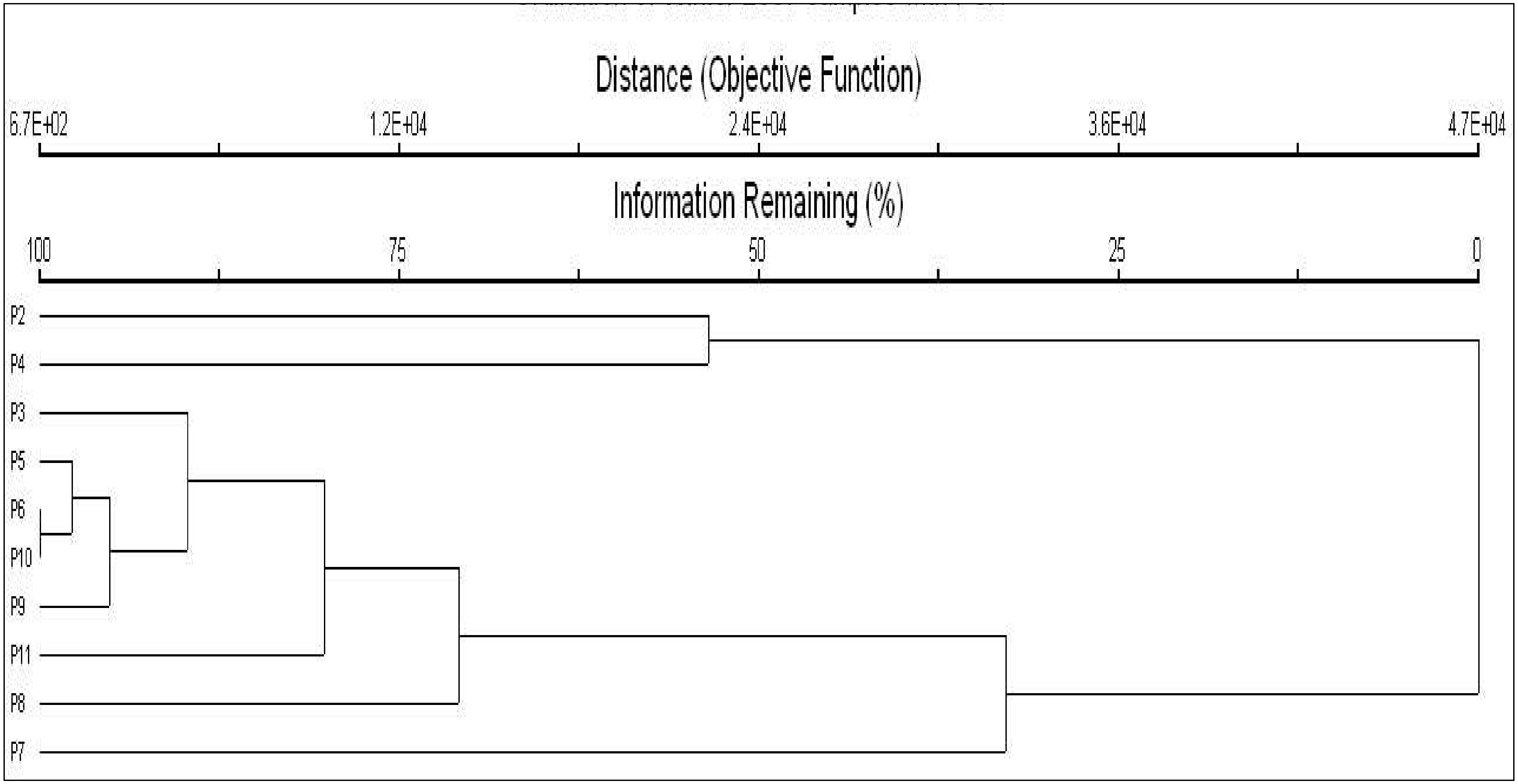


FIGURE 10: HIERARCHICAL CLUSTER ANALYSIS DONE USING EUCLIDIAN DISTANCE TO DETERMINE ASSOCIATION BETWEEN SPECIES COMPOSITION OF POOLS IN WINTER 2007.

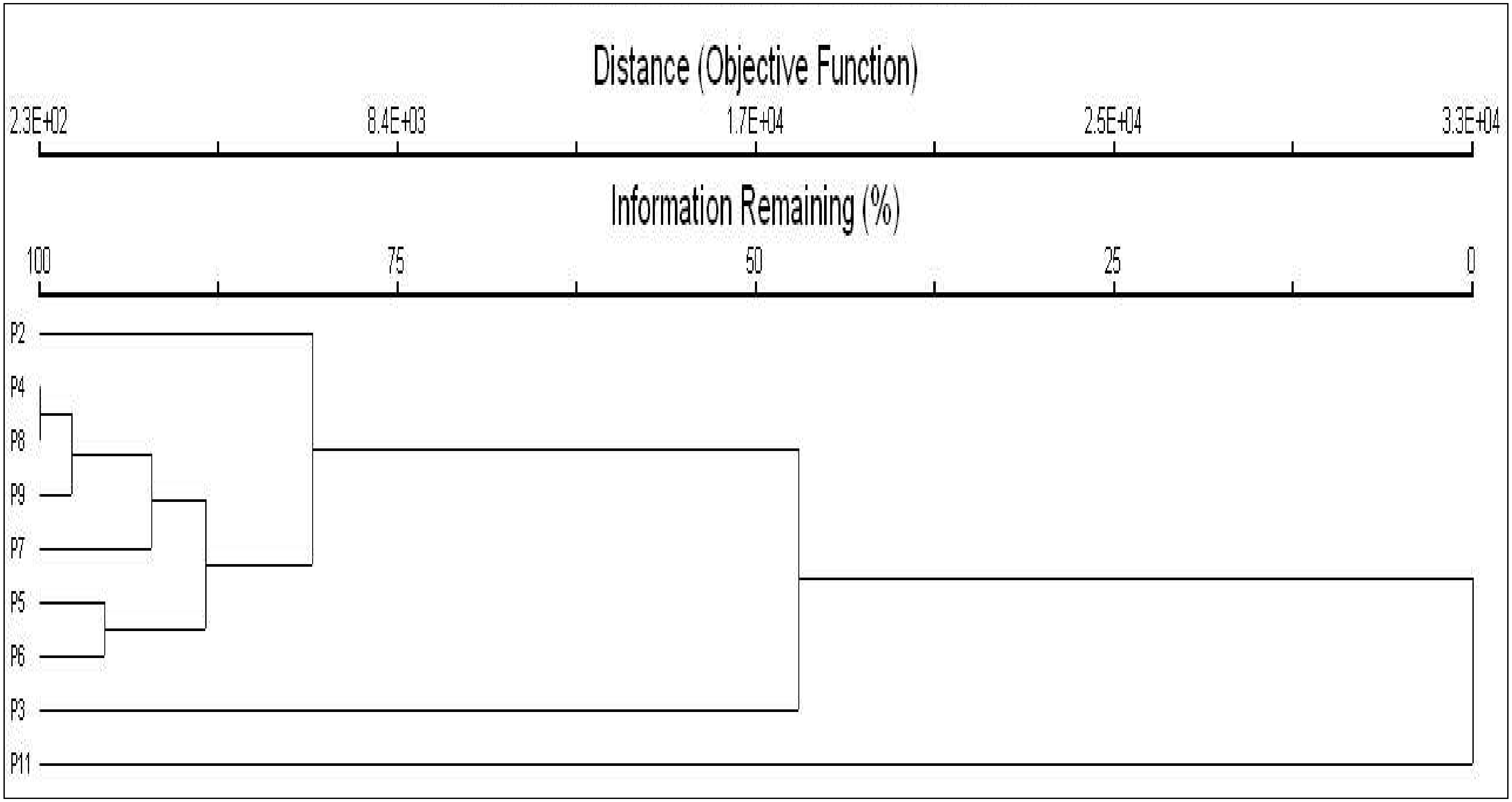


FIGURE 11: HIERARCHICAL CLUSTER ANALYSIS DONE USING EUCLIDIAN DISTANCE TO DETERMINE ASSOCIATION BETWEEN SPECIES COMPOSITION OF POOLS IN SPRING 2007.

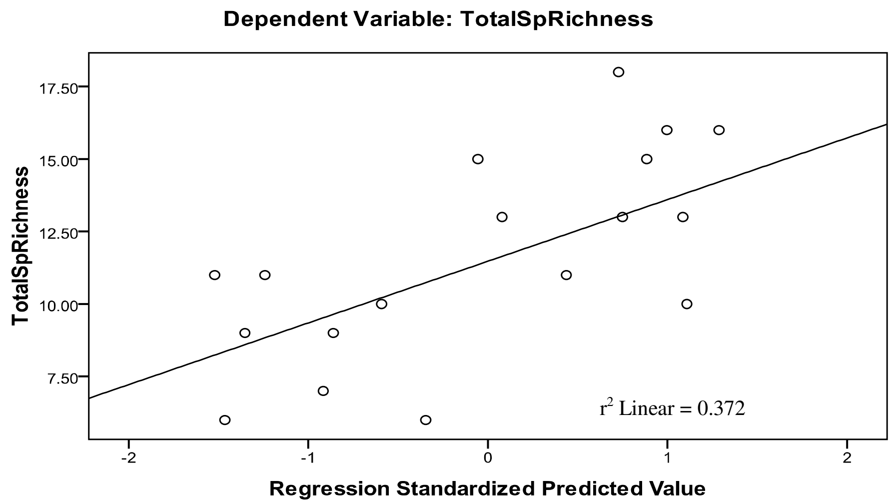


Figure 12: BEST FIT MODEL OF LINEAR REGRESSION ANALYSIS CONDUCTED TOOBSERVE THE EFFECT OF TEMPERATURE CHANGE ON TOTAL SPECIES RICHNESS OF THE POOLS SEASONALLY.

APPENDIX

APPENDIX A: Mean densities of macroinvertebrate species found in the 10 pools in winter 2007; mean values of 3 samples.

Species	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7	Pool 8	Pool 9	Pool 10	Pool 11
Amphipoda										
Crangonyctidae										
Crangonyx sp.	4	58	0	0	0	4	78	19	58	0
Coleoptera										
Ptilodactylidae										
Anchytarsus bicolor	4	8	0	0	0	0	0	0	0	8
Collembola										
Isotomurus tricolor	0	0	0	0	8	4	0	4	8	12
Podura aquatica	0	0	0	12	0	12	4	31	0	4
Sminthures aquaticus	0	0	0	4	16	0	0	12	4	8
Copepoda										
Cyclopidae										
Cyclops sp.	143	271	562	0	89	43	116	19	78	16

Calanidae										
Epischura sp.	0	0	0	0	0	0	12	0	0	0
Senecella sp.	58	78	213	0	54	0	140	8	19	0
Harpacticoida	0	16	19	0	58	0	4	0	43	27
Cladocera										
Daphnia sp.	0	0	0	0	0	353	318	0	0	151
Diptera										
Chaoboridae										
Chaoborus	0	0	4	0	0	12	0	0	0	0
Dolichopodidae	8	31	4	0	4	0	16	19	12	4
Elmidae	0	0	8	0	0	0	0	0	0	0
Tabanidae	0	0	0	0	0	0	0	4	0	0
Chironomidae										
Chironominae										
Endochironomus sp.	12	105	16	12	27	12	23	167	19	31
Glypotendipes sp.	0	0	0	0	0	0	0	8	0	0
Goeldichironomus sp.	0	0	0	0	0	4	0	0	0	0
Phaenospectra sp.	0	4	0	105	23	0	0	0	0	16

Polypedilum sp.	0	16	0	50	0	89	16	0	0	23
Stictochironomus sp.	0	19	0	0	0	0	0	0	0	0
Orthocladinae										
Parachaetocladius sp.	0	0	0	0	16	0	8	0	0	0
Xylotopus sp.	0	12	50	0	19	50	12	12	8	105
Syrphidae										
Eristalis tenax	4	0	0	0	0	0	0	4	0	4
Hydrachnidia										
Water mites	612	236	465	109	136	62	4	163	186	155
Hemiptera										
Macroveliidae sp.	0	0	0	0	0	0	0	0	0	4
Isopoda										
Caecidotea sp.	4	16	0	4	0	0	0	66	0	0
Microcharon sp.	8	19	12	0	0	0	0	31	43	8
Oligochaeta	0	27	0	12	16	4	8	58	81	23
Ostracoda	4	62	143	12	105	601	35	0	31	310
Total mean density	**860**	**977**	**1496**	**318**	**570**	**1248**	**791**	**624**	**589**	**907**

APPENDIX B: Mean densities of macroinvertebrate species found in the 10 pools in spring 2007; mean values of 3 samples.

Species	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7	Pool 8	Pool 9	Pool 10	Pool 11
Amphipoda										
Crangonyctidae										
Crangonyx sp.	0	0	0	0	0	4	8	0	0	0
Coleoptera										
Dytiscidae										
Copelatus sp.	0	35	0	0	0	0	0	12	0	0
Derovatellus sp.	0	0	0	0	0	0	0	0	0	8
Hydrosporus sp.	0	0	0	16	0	4	0	0	0	0
Ptilodactylidae										
Anchytarsus bicolor	0	0	0	0	4	0	0	0	0	4
Collembola										
Podura aquatica	4	16	0	4	4	4	0	0	0	0
Sminthures aquaticus	16	0	0	0	8	0	4	0	0	35
Copepoda										

Cyclopidae										
Cyclops sp.	0	0	62	19	0	35	16	0	0	16
Harpacticoida	0	0	0	4	0	0	0	0	0	23
Cladocera										
Daphnia sp.	0	0	0	0	0	0	27	0	0	605
Diptera										
Dolichopodidae	0	19	31	0	12	0	31	4	0	12
Chironomidae										
Chironominae										
Chironomus sp.	0	0	0	136	124	0	0	0	0	109
Endochironomus sp.	0	151	39	0	0	0	31	159	0	0
Goeldichironomus sp.	0	19	0	0	0	0	0	0	0	0
Phaenospectra sp.	0	8	12	0	0	0	0	0	0	0
Polypedilum sp.	0	0	0	0	16	0	19	0	0	16
Xenochironomus sp.	0	4	0	0	0	0	0	0	0	0
Orthocladinae										
Xylotopus sp.	0	4	12	27	16	0	66	0	0	43
Heleneilla sp.	0	4	0	0	0	0	0	0	0	0

Hydracarina										
Water mites	357	155	50	85	229	0	66	101	0	225
Isopoda										
Caecidotea sp.	0	0	0	0	0	0	0	0	0	12
Microcharon sp.	0	0	0	4	0	4	0	0	0	0
Oligochaeta	19	562	8	0	0	0	0	19	0	12
Ostracoda	16	0	8	19	0	128	4	0	0	12
Total mean density	**411**	**977**	**221**	**314**	**411**	**178**	**271**	**295**	**0**	**1128**

APPENDIX C: Mean densities of macroinvertebrate species found in the 3 pools in winter 2008; mean values of 3 samples.

Species	Pool 2	Pool 5	Pool 7
Amphipoda			
Crangonyctidae			
Crangonyx sp.	0	43	12
Coleoptera			
Dytiscidae			
Copelatus sp.	4	0	0
Collembola			
Podura aquatica	0	0	12
Sminthures aquaticus	4	0	0
Copepoda			
Cyclopidae			
Cyclops sp.	705	0	85
Diptera			
Dolichopodidae	8	8	0
Chironomidae			

Chironominae			
Endochironomus sp.	27	159	0
Phaenospectra sp.	4	19	0
Polypedilum sp.	0	0	12
Stictochironomus sp.	0	12	0
Orthocladinae			
Xylotopus sp.	8	16	4
Isopoda			
Caecidotea sp.	8	12	0
Microcharon sp.	12	12	0
Total mean density	**779**	**279**	**124**

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